

TAXONOMIC STUDIES IN *PELARGONIUM*,

SECTION *HOAREA* (GERANIACEAE)

by

ELIZABETH M. MARAIS

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ELIZABETH M. MARAIS

Dissertation presented for the Degree of Doctor of Philosophy
at the University of Stellenbosch.

Promoter: Professor Dr. J.J.A. van der Walt

March 1994

Reprinted by The Geraniaceae Group
March 2000

Best wishes

Bettie Marais.

PUBLICATION DATA

AUTHOR: **Elizabeth M. Marais.**

ARTIST: Ellaphie Ward-Hillhorst.

For other acknowledgements see Acknowledgments, p.341.

Published with the kind permission of:

the author, Dr.E.M.Marais;

AND

Professor Dr.J.J.A. van der Walt, then Chairman, Department of Botany,
University of Stellenbosch.

Originally published by: "The University of Stellenbosch"

Date original publication: March 1994.

Note that while it was ostensibly "ined" (not published) copies
have been distributed to persons in South Africa, U.S.A., Germany, England,
and Czech Republic who were not on the original Board of Invigilation to
which Dr.Marais submitted copies for her PhD, and that in international law
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March 1994.

This is a facsimile reprint Edition

(with print data, "contents - tables & figures" & page numbers added, and
place of official publication of those species "new" in the Thesis which
were "ined" at the time, added to the reprinted Index).

Date published: March 2000.

Published by: *The Geraniaceae Group* in England.

Printed by: R.Clifton.

Copyright: Dr.E.M.Marais, Botany Department, University of Stellenbosch.

ISBN: 1-899742-42-5.

ABSTRACT

Fifty nine species were studied in this taxonomic treatment of section *Hoarea* (Sweet) DC. of the genus *Pelargonium* L'Hérit., which was last revised by Knuth in 1912. The majority of species occur in the winter rainfall area of the south-western Cape, but some species occur in the eastern Cape, a region of winter and summer rainfall. A few species also occur in the summer rainfall area in the central Karoo.

Morphological, leaf anatomical, palynological and geographical data were studied in order to delimit the taxa and to determine their relationships. Eight new species were described and several name changes were made. Diagnostic features of the section are the regularly or turnip-shaped tubers with numerous dark brown peeling tunics or periderms and apically a short flattened stem from which the leaves and scape emerge. The zygomorphic flowers are almost sessile, because the pedicels are very short (0,5--1 mm) and the hypanthia long (6--100 mm). A large variation occurs in leaf form and floral structure, and the section is divided in 14 different floral groups, mainly based on the structure of the androecium and the tectum of the pollen grains, although petal form and size are also considered in clustering the species.

Section *Hoarea* with its deciduous geophytes and sometimes extremely zygomorphic flowers, exhibits advanced morphological characters. Because of the large variation in the structure of the androecium, pollination biology was probably one of the major driving forces in the evolution of the section, and the annual rainfall plays an important role in the distribution patterns of the different species.

UITTREKSEL

Neën en vyftig spesies is bestudeer in hierdie taksonomiese ondersoek van seksie *Hoarea* (Sweet) DC. van die genus *Pelargonium* L'Hérit., wat laas deur Knuth (1912) hersien is. Die meerderheid van die spesies kom in die winterreënstreek van die suidwes Kaap voor, maar sommige spesies word ook in die Oos-Kaap, wat 'n winter- en somerreënstreek is, aangetref. Enkele spesies kom in die somerreënstreek van die sentrale Karoo voor.

Morfologiese, blaaranatomiese, palinologiese en geografiese data is bestudeer om die verskillende taksons af te baken, en terselfdertyd verwantskappe tussen die onderskeie spesies te bepaal. Agt nuwe spesies is beskryf en verskeie naamsveranderinge is gemaak. Diagnostiese kenmerke van die seksie is die reëlmatig gevormde of raapvormige wortelknol met verskeie afskilferende donkerbruin periderms en apikaal 'n verkorte stingel waaruit blare en 'n bloeispil groei. Die sigomorfe blomme is byna sittend, aangesien die blomstele uiters kort is (0,5--1 mm) en die hipantiums relatief lank (6--100 mm). 'n Groot variasie in blaarvorm en blomstruktuur kom voor, en die seksie word in 14 verskillende blomvorms verdeel. Hierdie blomvorms is hoofsaaklik gebaseer op die struktuur van die andresium en tektum van die stuifmeelkorrels, alhoewel kroonblaarvorm en -grootte ook 'n rol gespeel het in die onderverdeling van die seksie.

Seksie *Hoarea* met sy bladwisselende geofiete en soms uiters sigomorfe blomme, vertoon gevorderde morfologiese kenmerke. Die groot variasie in die struktuur van die andresium dui op 'n moontlike prominente rol wat die bestuifwingsbiologie gespeel het in die evolusie van die seksie, en die jaarlikse reënval speel 'n belangrike rol in die verspreidingspatrone van die verskillende spesies.

Declaration

I, the undersigned, hereby declare that the work contained in this dissertation is my own original work and has not previously in its entirety or in part been submitted at any university for a degree

E. M. Marais

21 - 2 - 1994

Signature

Date

We must never conceal from ourselves that our concepts are creations of the human mind which we impose on the facts of nature, that they are derived from incomplete knowledge, and therefore will never exactly fit the facts, and will require constant revision as knowledge increases.

A.G. Tansley (1920)

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CHAPTER 1

INTRODUCTION

Section *Hoarea* (Sweet) DC. is the largest section of the genus *Pelargonium* L'Hérit. comprising more than 70 species. It consists of deciduous geophytes with regularly shaped tubers with dark brown peeling tunics or periderms, and apically a dense crown of petiole remains. The tuber is a root with apically a short flattened stem from which the leaves and scape emerge (Marais 1989a). Although the flowers of the majority of species in this section are rather small and dull-coloured, the large number of flowers per plant causes many of them being a spectacular sight when in flower. A small number of species does have large, bright-coloured and very attractive flowers. Unfortunately, because of the geophytic habit, these plants have a limited horticultural potential. They flower once a year, for a relatively short period, after which the leaves and scapes die away.

Sweet (1820) accommodated all *Pelargonium* species with turnip-shaped tubers, five petals and recurved sepals in the genus *Hoarea*. The name commemorates Sir Richard C. Hoare who probably had the largest collection of Geraniaceae in England at the time of Sweet's publication. Sweet was also obliged to him for many useful observations on the Geraniaceae. Sweet (1820) accommodated a second group of species with turnip-shaped tubers in the genus *Dimacria*, in allusion to the two anterior fertile stamens being twice the length of the rest (Don 1831). This genus was distinguished from *Hoarea* by the erect sepals and the incurved staminodes. Another genus with the same habit but with four perfect stamens only, the monotypic genus *Grenvillea*, was also described by Sweet (1825). Harvey (1860) included both *Dimacria* and *Grenvillea* in the section *Hoarea*. Yet another genus with turnip-shaped tubers and flowers with only two petals was described by Sweet (1824) as *Seymouria*, named in honour of Lady Seymour. This genus was transferred to sectional rank by Harvey (1860).

In the last revision of *Pelargonium*, published in 1912, Knuth divided the genus into 15 sections. In this he followed Harvey's (1860) revision in *Flora Capensis*. Both of them regarded the species with the more or less turnip-shaped tubers as belonging to two different sections, based on the number of petals present. Section *Hoarea* represents species with four- or five-petalled flowers (Sweet's genera *Hoarea*, *Dimacria* and *Grenvillea*), whereas section *Seymouria* consists of species with two-petalled flowers. Because of the similarities in growth form of these two sections as well as the similarities in the floral structure of all the species in section *Seymouria* and that of some species of

section *Hoarea* (*P. auritum* (L.) Willd., *P. bubonifolium* (Andr.) Pers. and *P. parvipetalum* E.M. Marais), these two sections are best regarded as one, namely section *Hoarea* (Marais 1989a).

Two species of the present section *Hoarea*, namely *Geranium pinnatum* L. and *G. auritum* L. were already published in Linnaeus's *Species Plantarum* in 1753. Following this publication, several more species were described by different authors. Sweet (1820), by describing the genus *Hoarea*, was the first to accommodate all the species with turnip-shaped tubers in a taxonomic unit of its own. De Candolle (1824) regarded this genus as a section of *Pelargonium*, a point of view followed by Harvey (1860) and Knuth (1912). Although section *Hoarea* does not represent the only tuberous species in *Pelargonium*, the subterranean flaking tuber with the short flattened stem, from which leaves and a scape emerge is distinctive for *Hoarea* and is unique for *Pelargonium*. As far as the floral structure is concerned, *Hoarea* shows little relationship with the rest of the genus (Marais 1981) and can be regarded as a natural taxon within the genus *Pelargonium*.

In respect to leaf form, Knuth (1912) divided section *Hoarea* into three subsections:

- Integra*: Leaves entire, and leaves entire and laciniate.
- Trilobata*: Leaves trilobate and tripartite.
- Pinnatifida*: Leaves pinnatifid.

Because of the variation in leaf incision within one species and because of the heteroblastic leaf development occurring in many species, this subdivision of the section is unacceptable to me. It is also generally accepted that vegetative characters are often regarded as unreliable evidence, because in many cases superficially similar morphological features are found in quite unrelated plants (Stace 1980). Stuessy (1990) regarded vegetative features to be more plastic and variable because of their numerous functions, and therefore more difficult to be used for taxonomic purposes. On the other hand it is well known that floral characters have been, and still are, those most used in the classification of flowering plants (Stace 1980). Therefore, in this taxonomic treatment of section *Hoarea* the emphasis was shifted to the floral features and especially to that of the androecium and the petals.

Knuth (1912) described a number of new species with outstanding diagnostic characters, but unfortunately he did not mention these characters in his descriptions, for example the very long staminodes of *P. fumariifolium* Knuth. Knuth never visited South Africa and studied only herbarium specimens. Knuth (1912) as well as Harvey (1860) inadvertently described new species which had been previously described by other taxonomists. The

problem in both cases was that herbarium specimens are difficult to relate to illustrations without detailed descriptions. I am convinced that for the taxonomic revision of this section, studying and collecting plants in their natural habitat and cultivating them in the garden is a necessity. Another advantage in my study of these plants, was the availability of the superb drawings of Ellaphie Ward-Hilhorst, without which this study would have been almost impossible.

Problems that complicated this study were the large number of species, the poor herbarium specimens, including poor type specimens, specimens without leaves or without flowers, in some cases the small number of specimens per species available, and also the small populations in which some of the species occur. This resulted in a very complicated nomenclature for this section.

The aim of this study was the taxonomic revision of section *Hoarea*, which, in the first place was the delimitation of the different species. Because of the large number of species in the section, a second aim and one which I regard as very important, was the subdivision of the section into smaller taxonomic units. To achieve this, macromorphological, anatomical and palynological characters were studied. Living plants were studied in their natural environment as well as in the Botanic Garden. This was supplemented by the study of a large number of herbarium specimens. Karyological studies are currently undertaken by Prof. F. Albers and co-workers at the Westfälische Wilhelms-Universität, Münster, and Dr M. Gibby at the Natural History Museum, London, and are not included here.

Because of the large number of species in this section, only taxa of which living material was available, were included. Poorly known species and species of which no living material could be found, were excluded from the study and listed in chapter 8 of this thesis. For some of these species no type specimens could be traced, for others the type specimens are so poor that the species concept is very difficult to define. A number of herbarium specimens, which could not be identified and which might be undescribed species, do exist, but were not included in this study. Of the living plant material which could not be matched with any described species, eight new species were described. Because of the exclusion of several species of this section, and without the results of the karyological studies, this revision should rather be regarded as an attempt to bring about a framework for the subdivision of the section. This will simplify the study of the unidentified specimens and also those species of which the species concept is difficult to define. With karyological and chemotaxonomical data known, the subdivision of the section should be finalized, and subsections should be demarcated with more confidence.

CHAPTER 2

MATERIAL AND METHODS

This revision is based on macromorphological, leaf anatomical and palynological data as well as the distribution patterns of the different species.

An extensive literature study was undertaken. All available literature since 1753 on the Geraniaceae and on the Cape Flora were searched for names and with the help of a computer and the PC-File⁺ database programme these data were sorted. The following fields were used: species name, author, date of publication, publication, basionym, taxon, type, type locality, herbarium (type specimen). This enabled me to extract all the names for a specific taxon. At the same time the oldest basionym could be determined. For four names no type material could be traced, and for several others the type specimens or the iconotypes were so poor that the interpretation of them are almost impossible. A list of these insufficiently known species is included in chapter 8. Fifty nine species, of which one is subdivided into two varieties, are included in this study. Type specimens or iconotypes for all species included and for all synonyms recognized, were studied. Lectotypes were designated where necessary. Living material of all the included taxa were available and were illustrated by Ellaphie Ward-Hilhorst.

Extensive field work was done to study plants in their natural environment. Plants were collected in the field and cultivated in the garden. Most of the species of section *Hoarea* flower in summer after the leaves have been shed, therefore herbarium specimens without leaves or without flowers are quite common. This results in incomplete herbarium specimens and in several cases very poor type specimens. Another factor contributing to the poor herbarium record is the fact that species of this section usually occur in very small populations. For this project proper specimens were prepared from cultivated plants in the garden. Leaves and flowers were collected at different stages.

Herbarium specimens were studied at, or obtained on loan, from the following herbaria (abbreviations are from Holmgren and Keuken 1974):

B	Botanic Garden & Botanic Museum, Berlin Dahlem, Berlin.
BLFU	Geo. Potts herbarium, University of the Orange Free State, Bloemfontein.
BM	The Natural History Museum, London.
BOL	Bolus Herbarium, University of Cape Town, Cape Town.
BOL-FOURCADE	Fourcade Herbarium, University of Cape Town, Cape Town.

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CGE	Herbarium, Botany School, University of Cambridge, Cambridge.
E	Herbarium, Royal Botanic Garden, Edinburgh.
G	Conservatoire and Botanic Garden, Genève.
G-BURM	Burman Herbarium, Conservatoire and Botanic Garden, Genève.
G-DC	De Candolle Herbarium, Conservatoire and Botanic Garden, Genève.
GRA	Herbarium, Albany Museum, Grahamstown.
K	Royal Botanic Gardens, Kew.
KMG	Herbarium, Alexander McGregor Museum, Kimberley.
L	Rijksherbarium, Leiden.
LINN	Herbarium, Linnean Society, London.
M	Herbarium, Botanische Staatssammlung, München.
MA	Herbarium, Botanic Garden, Madrid.
MEL	National Herbarium of Victoria, Royal Botanic Garden, Melbourne.
MO	Herbarium of Missouri Botanic Garden, Saint Louis.
NBG	Compton Herbarium, National Botanical Institute, Cape Town.
NH	Natal Herbarium, National Botanical Institute, Durban.
OXF	Fielding-Druce Herbarium, Department of Botany, Oxford University, Oxford.
P	Herbarium, Museum of Natural History, Paris.
P-JU	Jussieu Herbarium, Museum of Natural History, Paris.
P-LA	Lamarck Herbarium, Museum of Natural History, Paris.
PRE	National Herbarium, National Botanical Institute, Pretoria.
S	Herbarium, Swedish Museum of Natural History, Stockholm.
SAM	South African Museum Herbarium, National Botanical Institute, Cape Town.
SRGH	Government Herbarium, Harare, Zimbabwe.
STE	Herbarium, National Botanical Institute, Stellenbosch.
STEU	Herbarium, Department of Botany, University of Stellenbosch, Stellenbosch.
TCD	Herbarium, Trinity College, Dublin.
UPS	Herbarium, Institute of Systematic Botany, University of Uppsala, Uppsala.
W	Natural History Museum, Vienna.
WIND	Government Herbarium, Windhoek.
WU	Botanical Institute and Botanical Garden, University of Vienna, Vienna.
Z	Botanic Garden and Institute for Systematic Botany, University of Zürich, Zürich.

Macromorphology

Living specimens, collected in the field or as in most cases grown in the garden for at least one season, as well as herbarium specimens were studied for macromorphological data. Depending on the availability of the material, between five and ten herbarium

specimens for every taxon were studied in detail and measurements were taken. The descriptive terminology used in this study was based on that given by Radford *et al.* (1974).

Leaf anatomy

Leaf anatomical studies were performed on fresh material from plants growing in the garden for more than one season. This ensured that all the material studied was from plants growing for a considerable time under similar conditions. For the majority of species three or more specimens were studied (Table 4.7). This, however was not possible for all species and for *P. chelidonium* (Houtt.) DC., *P. proliferum* (Burm. f.) Steud., *P. caledonicum* L. Bol., *P. attenuatum* Harv. and *P. campestre* (Eckl. & Zeyh.) Steud. no living specimens were available at the time the anatomical study was undertaken.

Transverse sections of wax-embedded petioles and laminae were cut with a rotary microtome and stained with Alcian Green Safranin (Joel 1983). Sections were made through the middle part of the petiole and the laminae, or in the case of compound leaves the middle part of the pinnae.

Pollen morphology

Pollen grains of all the species were studied. For the majority of the species pollen grains were freshly collected in the garden, but in some cases also taken from herbarium specimens (Table 5.3). All pollen specimens were prepared using the acetolysis method (Radford *et al.* 1974) and studied with the light microscope after mounted in glycerine jelly, and with a JEOL JSM-35 scanning electron microscope, after sputter-coated with palladium. At least twenty-five pollen grains of each specimen were studied and measured.

Geographical distribution and ecology

The data on the geographical distribution of all herbarium specimens cited, were computerized, using the PC-File⁺ database programme. Geographical distribution of every specimen was cited according to the grid reference method proposed by Leistner & Morris (1976). A distribution map for every taxon was compiled from these data. Data on soil type and vegetation preferences as well as the flowering time were also obtained

from the herbarium sheets. Rainfall figures for the different species were compiled by comparing distribution maps with rainfall maps of Jackson (1961).

Taxonomy

The taxonomic treatment has been arranged according to the guide for contributors to the *South African Journal of Botany*. This includes the format for references to the literature and the specimens cited.

Cytological studies

Cytological studies are currently undertaken by Prof. F. Albers and co-workers at the Westfälische Wilhelms-Universität, Münster, and Dr M. Gibby at the Natural History Museum, London, and are not included here.

CHAPTER 3

MACROMORPHOLOGY

As stated by Stuessy (1990) morphology or the external form of an organism, has been and still is the type of data used most in plant classification. Morphological features have the advantage of being easily seen, and hence their variability has been much more appreciated than for other kinds of features. It is generally accepted that the floral features play an important role in angiosperm taxonomy, but vegetative characters can often be used to good effect. According to Stuessy (1990), vegetative characters are repeating units of structure without fixed numbers of parts, in contrast to floral features which are more definite in number. This he ascribed to the narrow but obvious important role of floral features in reproduction. He regarded the features of the vegetative organs to be more plastic and/or variable because of the numerous functions, and hence more difficult to use for taxonomic purposes. Nevertheless in section *Hoarea* leaves do reveal variation which can be useful in the taxonomic treatment of the section.

Tuber

According to Jones & Luchsinger (1987) growth habit of plants may be of primary usefulness in classification and vegetative underground structures such as rhizomes, corms, and bulbs may sometimes characterize a group. Both these statements are true in the case of section *Hoarea*, since the section is demarcated as deciduous geophytes with more or less regularly shaped tubers. If compared with other sections of *Pelargonium* with tuberous species, plants of this section have turnip-shaped or elongated tubers, with dark brown peeling tunics or periderms. The tuber is a root with apically a short flattened stem from which the leaves and a scape emerge. Sometimes the tap-root or lateral roots form series of underground tubers. The size of the main tuber varies from 10--150 mm in length and from 10--150 mm in diameter. In young plants the tuber usually produces only one scape, whereas older plants are inclined to produce two or even more scapes. In *P. appendiculatum* (L. f.) Willd. numerous stem divisions are very prominent. This extensive branching is probably stimulated by grazing of sheep and antelope, forming clumps up to half a meter in diameter. The annual increments, terminated by leaves, are clearly distinguishable on these branches. To a lesser extent this same type of stem divisions occurs in *P. triphyllum* Jacq. In older plants of *P. fasciculaceum* E.M. Marais extensive branching of the fleshy roots and the formation of numerous stem-growing points, result in large colonies of these plants (Marais 1991). Colony formation, however, is not typical for section *Hoarea*. Although the morphology

of the tuber is a distinctive character by which the section is demarcated from the rest of the genus, the morphology of the tuber is of little or no taxonomic value within the section itself.

Leaves

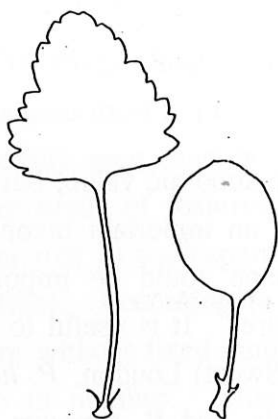
In some taxa vegetative features are of little taxonomic value, but in species with similar flower or fruit structures, leaf shape can be an important taxonomic feature (Jones & Luchsinger 1987). In *Hoarea* the leaf shape could be important for identification purposes in species with similar floral structures. It is useful to distinguish between *P. ellaphieae* E.M. Marais and *P. asarifolium* (Sweet) Loudon, *P. heterophyllum* Jacq. and *P. trifoliolatum* (Eckl. & Zeyh.) E.M. Marais, and *P. carneum* Jacq. and *P. radiatum* (Andr.) Pers. (Figure 3.1). The problem however, is that leaves of most *Hoarea* species may wither and die before flowering, and are often lacking on specimens with flowers and fruits. A second problem concerning leaf form is the variation in leaf incision within one species, and a third problem is the heteroblastic leaf development that occurs in many species. According to Gould (1993) different hypotheses have been developed to explain leaf heteroblasty among New Zealand's flora, of which the possibility that juvenile forms are adaptations, evolved in response to browsing by animals, could be applied to species of *Hoarea*, since these plants are heavily grazed. A second hypothesis that heteroblastic species have arisen from interspecific hybridization of ancestral homoblastic species could also be true for section *Hoarea*, because in all groups hybridization remains always a possibility. Nevertheless, heteroblasty causes difficulties in demarcating species as was found in the highly variable species *Begonia dregei* Otto & Dietr. (McLellan 1990). The first taxonomist recognized numerous different species in respect to the degree of leaf incision, while the second taxonomist placed all these names in synonymy (McLellan 1990). In the study of section *Hoarea* a more conservative way regarding heteroblasty was followed; lumping rather than splitting species as in *P. longifolium* (Burm. f.) Jacq., *P. dipetalum* L'Hérit. and *P. proliferum*. Leaf size in section *Hoarea* is also of little taxonomic value since in species with prostrate leaves the older leaves are larger with longer petioles than the younger ones, forming a rosette. This complicates identification of species on leaf characters alone. Despite these problems there is somehow a pattern in leaf form and leaf incision (Figure 3.1) that can be useful to distinguish between species with similar floral structures. Twelve basic patterns for the leaf shape are recognized, and due to differences in texture of the laminae and the orientation or the length of the petioles these groups are subdivided. In Figure 3.1 species with similar leaf structures are grouped together.

Figure 3.1 Species of section *Hoarea* arranged according to leaf form.

1. Simple, cordiform, prostrate

- P. punctatum*
P. triandrum
P. curviandrum
P. oblongatum
P. githagineum

P. asarifolium



2. Simple (ovate to cordiform) to tripartite or trifoliate, prostrate

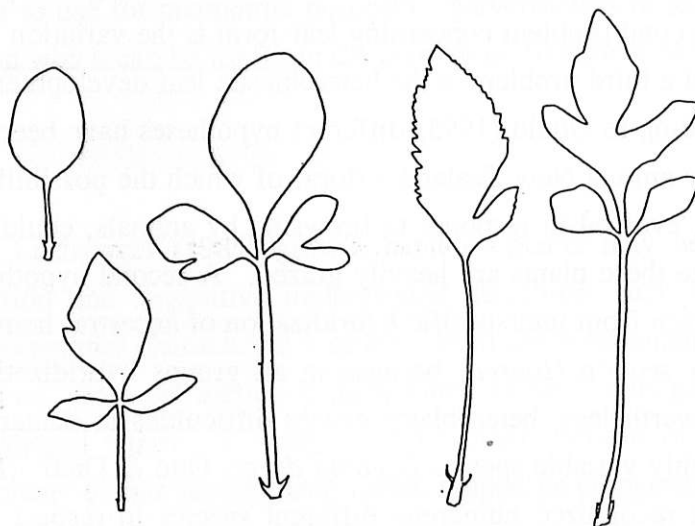
- P. heterophyllum*
P. tenellum
P. chelidonium

P. moniliforme
P. vinaceum

P. nervifolium
P. triphyllum

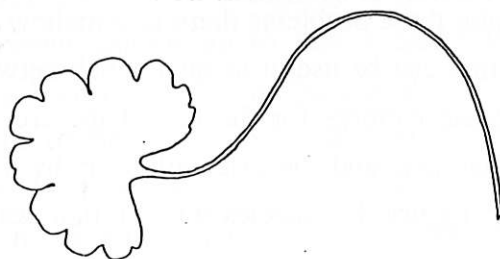
P. campestre
P. aestivale

P. grenvilleae
P. radiatum
P. nummulifolium



3. Simple (palmately veined), reniform, petiole curved

- P. nephrophyllum*



4.

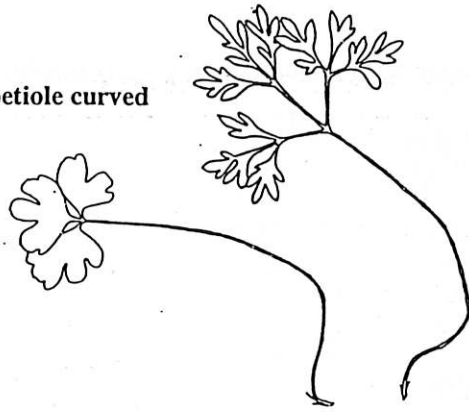
5.

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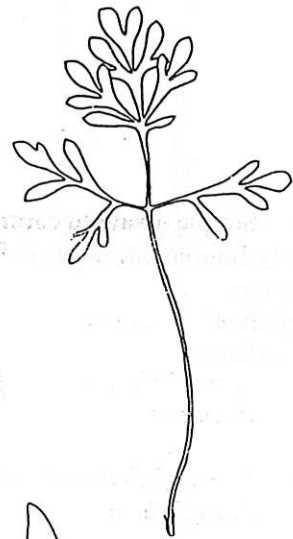
4. **Palmately compound, ternate to tripinnatisect, petiole curved**

P. ternifolium
P. reflexum
P. fergusoniae



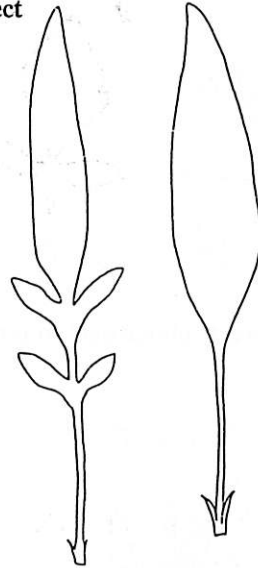
5. **Palmately compound, ternate to tripinnatisect, petiole erect**

P. luteolum
P. gracillimum
P. attenuatum
P. angustipetalum



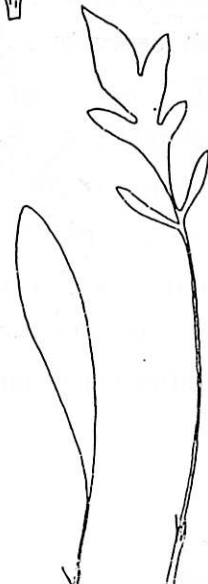
6. **Simple to tripartite or trifoliolate, lanceolate, petiole erect**

P. longiflorum
P. radicum
P. ellaphieae



7. **Simple to pinnatisect or pinnately compound, lanceolate, petiole erect**

P. pilosellifolium



11. Pinnately compound, erect, pinnate to irregularly bi- or tripinnatisect

P. auritum
P. incrassatum

P. fissifolium
P. petroselinifolium
P. aristatum
P. luteum
P. carneum

P. bubonifolium
P. parvipetalum

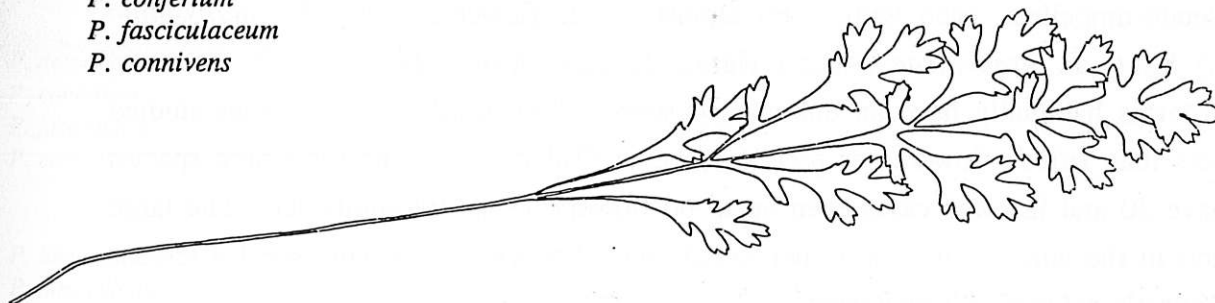
P. appendiculatum
P. caroli-henrici
P. rubiginosum

P. caledonicum
P. rapaceum



12. Pinnately compound, erect, irregularly bi- or tripinnatisect, aciculatum group

P. aciculatum
P. confertum
P. fasciculaceum
P. connivens



Different types of trichomes occur on the leaves, and different combinations of glandular hairs (short, medium length and long) and non-glandular hairs (long soft patent hairs, appressed curly hairs, appressed stiff hairs, patent stiff hairs and bristles) occur. Thus the indumentum of the leaf varies, and can be useful as a diagnostic tool rather than using it as an aid to establish interrelationships of taxa. This is based on the statement by Metcalfe & Chalk (1950) that the value for systematic purposes of different types of trichomes, is lessened by the fact that the same kind of trichome occur in unrelated groups, thus making it reasonably certain that the same type of hair must have been evolved along independent lines. Therefore trichomes do not have a significant influence

on phylogenetic thought. An outstanding character of the indumentum of section *Hoarea* is that appressed hairs are always distally orientated.

One of the diagnostic characters of section *Hoarea* is the stipules which are adnate to the petioles. In species with prostrate leaves the stipules are rather short and in most cases triangular in outline, whereas in species with erect or erecto-patent leaves the stipules are long and usually subulate. The length of the stipules often varies conspicuously within one population of a species. This variation can be ascribed to the depth of the tuber below ground level; the deeper the tubers are situated the longer the stipules (Marais 1993). Only in *P. appendiculatum* the form of the stipules is diagnostic within section *Hoarea*.

Inflorescence

The flowers of *Pelargonium* are borne in pseudo-umbels or umbelliform dichasiums (Wyatt 1982) with the older flowers in the centre and the younger ones on the periphery of the inflorescence. In section *Hoarea* flowers are borne on a scape. Some plants bear only a single scape, whereas others, usually older plants, have more than one scape per plant, due to the presence of more than one stem-growing point per tuber. In the majority of species the scape is branched, forming a compound inflorescence with 2--8(-12) pseudo-umbellets, each with 3--60 almost sessile flowers. Only *P. incrassatum* (Andr.) Sims, *P. grenvilleae* (Andr.) Harv., *P. moniliforme* Harv. and *P. vinaceum* E.M. Marais habitually have an unbranched scape. Two thirds of the species studied have less than fifteen flowers per pseudo-umbellet (Table 3.1). The remaining species may have 30 and in some cases even up to 60 flowers per pseudo-umbellet. The large variation in the number of flowers per pseudo-umbellet within the same species lessens the diagnostic value of this character.

The flower buds, flowers and the fruits are erect. The height of the plants when in flower varies from 80--500 mm above ground level. The scape with the flowers usually rise above the leaves.

Table 3.1 Number of flowers per pseudo-umbel or pseudo-umbellet of the different *Hoarea* species.

Species	0	20	40	60	80
<i>P. aestivale</i>	— — — — —				
<i>P. fissifolium</i>	— — — — —				
<i>P. petroselinifolium</i>	— — — — —				
<i>P. aristatum</i>	— — — — —				

Table 3.1 Number of flowers per pseudo-umbel or pseudo-umbellet of the different *Hoarea* species (continue).

Species	0	20	40	60	80
<i>P. chelidonium</i>	-----				
<i>P. nervifolium</i>	----- -----				
<i>P. pinnatum</i>	-----				
<i>P. reflexum</i>	-----				
<i>P. heterlobum</i>	-----				
<i>P. attenuatum</i>	-----				
<i>P. angustipetalum</i>	-----				
<i>P. leptum</i>	-----				
<i>P. viciifolium</i>	----- -----				
<i>P. longifolium</i>	-----				
<i>P. fergusoniae</i>	-----				
<i>P. undulatum</i>	-----				
<i>P. longiflorum</i>	-----				
<i>P. proliferum</i>	-----				
<i>P. pilosellifolium</i>	-----				
<i>P. caledonicum</i>	-----				
<i>P. heterophyllum</i>	-----				
<i>P. tenellum</i>	-----				
<i>P. trifoliolatum</i>	----- -----				
<i>P. aciculatum</i>	----- ----- -----				
<i>P. confertum</i>	----- ----- -----				
<i>P. fasciculaceum</i>	----- ----- -----				
<i>P. connivens</i>	----- ----- -----				
<i>P. luteum</i>	----- -----				
<i>P. fumariifolium</i>	----- -----				
<i>P. incrassatum</i>	----- ----- ----- -----				
<i>P. grenvilleae</i>	----- ----- -----				
<i>P. moniliforme</i>	----- ----- -----				
<i>P. vinaceum</i>	----- -----				
<i>P. radicatum</i>	----- -----				
<i>P. appendiculatum</i>	----- -----				
<i>P. campestre</i>	-----				
<i>P. nephrophyllum</i>	-----				
<i>P. carneum</i>	-----				
<i>P. radiatum</i>	-----				
<i>P. nummulifolium</i>	-----				

Table 3.1 Number of flowers per pseudo-umbel or pseudo-umbellet of the different *Hoarea* species (continue).

Species	0	20	40	60	80
<i>P. luteolum</i>	_____				
<i>P. gracillimum</i>	_____				
<i>P. rapaceum</i>	_____				
<i>P. auritum</i> var. <i>auritum</i>	_____				
<i>P. auritum</i> var. <i>carneum</i>	_____				
<i>P. bubonifolium</i>	_____				
<i>P. parvipetalum</i>	_____				
<i>P. leipoldtii</i>	_____				
<i>P. ellaphieae</i>	_____				
<i>P. asarifolium</i>	_____				
<i>P. dipetalum</i>	_____				
<i>P. ternifolium</i>	_____				
<i>P. triphyllum</i>	_____				
<i>P. githagineum</i>	_____				
<i>P. caroli-henrici</i>	_____				
<i>P. rubiginosum</i>	_____				
<i>P. oblongatum</i>	_____				
<i>P. curviandrum</i>	_____				
<i>P. triandrum</i>	_____				
<i>P. punctatum</i>	_____				

Flower

Floral features are the most important characters in the classification of flowering plants. Being more constant than vegetative features, reproductive characters are generally more numerous and therefore provide more features to differentiate taxa. In addition these features are easily observed, and they are practical for use in keys and descriptions (Jones & Luchsinger 1987), therefore the emphasis in the taxonomic treatment of section *Hoarea* was on the floral structure.

Like most species of the genus *Pelargonium*, all species of section *Hoarea* have zygomorphic flowers. In almost all species the form and size of the posterior two petals

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differ obviously from the anterior three. The degree of zygomorphy is emphasized by the differences between the orientation of the posterior petals and those of the anterior ones. The androecium in all species is also zygomorphic.

Hypanthium

The hypanthium, typical for *Pelargonium*, is well developed in all *Hoarea* species. In all the species in section *Hoarea* the hypanthium is long (6--100 mm) in comparison with the very short pedicel (0.5--1 mm long). In the majority of species the hypanthium is straight, but in *P. incrassatum* and *P. grenvilleae* it is typically curved. The length of the hypanthium could be of diagnostic value in species with similar floral structures (Table 3.2; *P. aciculatum* E.M. Marais, *P. confertum* E.M. Marais, *P. fasciculaceum*, and *P. connivens* E.M. Marais; *P. fissifolium* (Andr.) Pers. and *P. petroselinifolium* G. Don; *P. luteolum* N.E. Br. and *P. gracillimum* Fourc.; and *P. radicum* Venten. and *P. appendiculatum*). On the other hand the length of the hypanthium does confirm relationships among species with similar floral structures like *P. proliferum*, *P. pilosellifolium* (Eckl. & Zeyh.) Steud. and *P. caledonicum* L.; *P. heterophyllum*, *P. tenellum* (Andr.) G. Don and *P. trifoliolatum*; *P. luteum* (Andr.) G. Don and *P. fumariifolium*; and *P. auritum* (L.) Willd. var. *auritum*, *P. auritum* var. *carneum* (Harv.) E.M. Marais, *P. bubonifolium* (Andr.) Pers., *P. parvipetalum* E.M. Marais, *P. leipoldtii* Knuth, *P. ellaphieae* E.M. Marais, *P. asarifolium* (Sweet) Loudon and *P. ternifolium* Vorster (Table 3.2). The diagnostic value of the hypanthium length, however, is lessened by the large variation in the length occurring in *P. aestivale* E.M. Marais (33--66 mm), *P. fissifolium* (28--65 mm), *P. pinnatum* (L.) L'Hérit. (11--35--45 mm), *P. longiflorum* Jacq. (10--15--44 mm), *P. moniliforme* (20--77 mm), *P. appendiculatum* (60--100 mm), *P. rapaceum* (L.) L'Hérit. (12--55 mm), *P. carneum* (29--35--75 mm), *P. radiatum* (30--62 mm), *P. oblongatum* Harv. (30--68 mm), most of them species with long hypanthia. In *P. dipetalum*, with usually short hypanthia (7--18 mm long), three populations with very long hypanthia (35--50 mm long) were found.

The indumentum of the hypanthium is often similar to that of the peduncle and sepals. The colour of the hypanthium varies from green to greenish red (*P. githagineum* E.M. Marais) or conspicuously wine-red (*P. moniliforme*, *P. vinaceum*, *P. caroli-henrici* B. Nord. and *P. rubiginosum* E.M. Marais). Both characters are of diagnostic value.

Table 3.2 The hypanthium length of the different species of section *Hoarea* (continue).

Species	10	20	30	40	50	60	70	80 mm
<i>P. nephrophyllum</i>		_____						
<i>P. carneum</i>			_____	_____	_____	_____	_____	
<i>P. radiatum</i>			_____	_____	_____	_____	_____	
<i>P. nummulifolium</i>			_____	_____	_____	_____	_____	
<i>P. luteolum</i>	_____	_____						
<i>P. gracillimum</i>	_____	_____	_____					
<i>P. rapaceum</i>	_____	_____	_____	_____	_____	_____	_____	
<i>P. auritum</i> var. <i>auritum</i>	_____	_____						
<i>P. auritum</i> var. <i>carneum</i>	_____	_____						
<i>P. bubonifolium</i>	_____	_____						
<i>P. parvipetalum</i>	_____	_____						
<i>P. leipoldtii</i>	_____	_____						
<i>P. ellaphieae</i>	_____	_____						
<i>P. asarifolium</i>	_____	_____						
<i>P. dipetalum</i>	_____	_____	_____	_____	_____	_____	_____	
<i>P. ternifolium</i>	_____	_____						
<i>P. triphyllum</i>	_____	_____						
<i>P. githagineum</i>	_____	_____						
<i>P. caroli-henrici</i>		_____	_____					
<i>P. rubiginosum</i>		_____	_____					
<i>P. oblongatum</i>			_____	_____	_____	_____	_____	
<i>P. curviandrum</i>		_____	_____					
<i>P. triandrum</i>		_____	_____					
<i>P. punctatum</i>		_____	_____					

Sepals

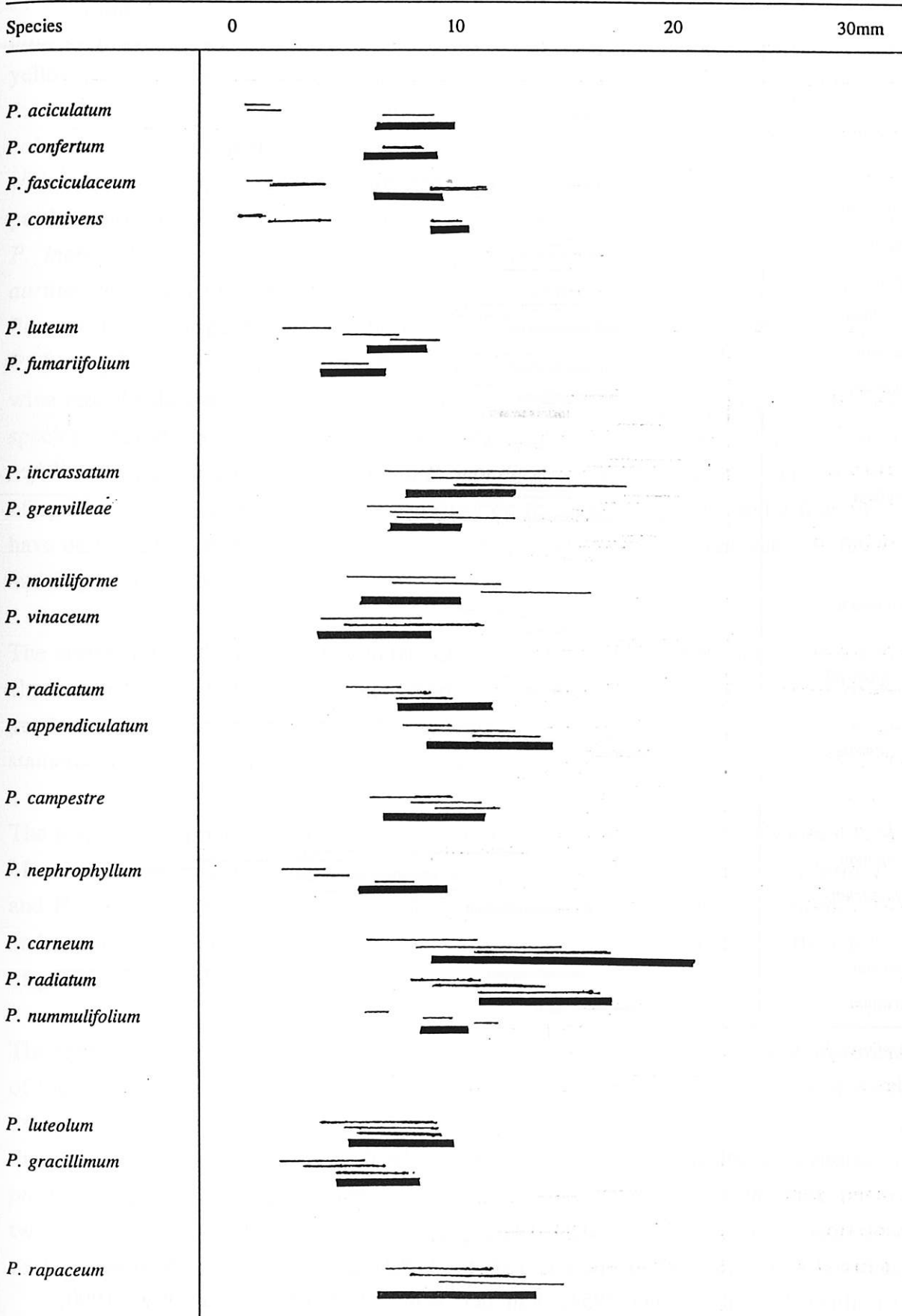
The calyx in section *Hoarea* is of little or no taxonomic value. All species have five sepals of which the posterior one is the widest. During anthesis all the sepals could be patent or all could be recurved, but often the posterior one remains erect, whereas the others are recurved. The relation between the length of the sepals and that of the stamens is an important character used in the delimitation of the different types of floral structures

(Table 3.3). The sepals are persistent and cover the developing fruit after fertilization, thus a character which could be used after the petals are dropped.

Table 3.3 The comparison between sepal length (▬) and stamen length (—) of the species of section *Hoarea*.

Species	0	10	20	30mm
<i>P. aestivale</i>		▬	—	
<i>P. fissifolium</i>		▬	—	
<i>P. petroselinifolium</i>		▬	—	
<i>P. aristatum</i>		▬	—	
<i>P. chelidonium</i>		▬	—	
<i>P. nervifolium</i>		▬	—	
<i>P. pinnatum</i>		▬	—	
<i>P. reflexum</i>		▬	—	
<i>P. violiflorum</i>		▬	—	
<i>P. attenuatum</i>		▬	—	
<i>P. angustipetalum</i>		▬	—	
<i>P. leptum</i>		▬	—	
<i>P. viciifolium</i>		▬	—	
<i>P. longifolium</i>		▬	—	
<i>P. fergusoniae</i>		▬	—	
<i>P. undulatum</i>		▬	—	
<i>P. longiflorum</i>		▬	—	
<i>P. proliferum</i>		▬	—	
<i>P. pilosellifolium</i>		▬	—	
<i>P. caledonicum</i>		▬	—	
<i>P. heterophyllum</i>		▬	—	
<i>P. tenellum</i>		▬	—	
<i>P. trifoliolatum</i>		▬	—	

Table 3.3 The comparison between sepal length (▬) and stamen length (—) of the species of section *Hoarea* (continue).



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Table 3.3 The comparison between sepal length (—) and stamen length (—) of the species of section *Hoarea* (continue).

Species	0	10	20	30mm
<i>P. auritum</i> var. <i>auritum</i>		[Stamen length bars from ~10 to ~25 mm]		
<i>P. auritum</i> var. <i>carneum</i>		[Sepal length bar from ~10 to ~15 mm]		
<i>P. bubonifolium</i>		[Stamen length bars from ~10 to ~15 mm]		
<i>P. parvipetalum</i>		[Sepal length bar from ~10 to ~15 mm]		
<i>P. leipoldtii</i>		[Stamen length bars from ~10 to ~15 mm]		
<i>P. ellaphieae</i>		[Stamen length bars from ~10 to ~15 mm]		
<i>P. asarifolium</i>		[Sepal length bar from ~10 to ~15 mm]		
<i>P. dipetalum</i>		[Stamen length bars from ~10 to ~15 mm]		
<i>P. ternifolium</i>		[Sepal length bar from ~10 to ~15 mm]		
<i>P. triphyllum</i>		[Stamen length bars from ~10 to ~15 mm]		
<i>P. githagineum</i>		[Sepal length bar from ~10 to ~15 mm]		
<i>P. caroli-henrici</i>		[Stamen length bars from ~10 to ~15 mm]		
<i>P. rubiginosum</i>		[Sepal length bar from ~10 to ~15 mm]		
<i>P. oblongatum</i>		[Stamen length bars from ~10 to ~25 mm]		
<i>P. curviandrum</i>		[Sepal length bar from ~10 to ~15 mm]		
<i>P. triandrum</i>		[Stamen length bars from ~10 to ~25 mm]		
<i>P. punctatum</i>		[Sepal length bar from ~10 to ~15 mm]		

Petals

Modifications in floral morphology can usually be related to the mode of pollination or specialized reproduction. Insect-pollinated plants, typically have large colourful, bisexual flowers (Jones & Luchsinger 1987). The showiness of the flowers attracts pollinators. Although *Hoarea* species, like most *Pelargonium* species, are probably insect-pollinated plants (Vogel 1954, Van der Walt, McDonald & Van Wyk 1990,

McDonald & Van der Walt 1992, Zietsman 1993), the majority of species have rather small white, cream-coloured, pale yellow or pale pink flowers. Only a few species like *P. incrassatum*, *P. nummulifolium* Salisb., *P. carneum*, *P. radiatum* have large bright pink or purple petals. *P. oblongatum* is another species with large flowers, but with yellow petals. Although smaller than the former, the pink flowers of *P. chelidonium* and those of *P. nephrophyllum* E.M. Marais are also very striking. *P. pilosellifolium*, *P. caledonicum*, *P. auritum* var. *auritum*, *P. ellaphieae* and *P. asarifolium* are all species with small flowers, but they still are striking because of the wine-red or nearly black petals. Flower colour is diagnostic in the case of *P. petroselinifolium*, *P. chelidonium*, *P. incrassatum*, *P. nephrophyllum*, *P. gracillimum*, *P. auritum* var. *auritum*, and *P. auritum* var. *carneum*. Although the majority of species in *Hoarea* have dull-coloured flowers, pollinator guides compensate for the lack of bright colours. In *P. longifolium*, *P. heterophyllum*, *P. trifoliolatum*, *P. moniliforme* and *P. vinaceum* prominent black or wine-red blotches occur on the posterior petals, which are also diagnostic in all these species. These markings also confirm a relationship between *P. heterophyllum* and *P. trifoliolatum*, and a relationship between *P. moniliforme* and *P. vinaceum*. The majority of species have wine-red feather-like markings on the posterior petals, and a few others have only dimly coloured V-shaped markings (*P. fasciculaceum*, *P. connivens*, *P. luteum* and *P. fumariifolium*).

The orientation of the petals varies in the different species. In the majority of species the claws form a floral sheath, in which short stamens are concealed. The apices of the petals are patent or recurved to different degrees, and depending on the length of the stamens, the latter protrudes from the flowers.

The majority of species have five-petalled flowers. Only one species, *P. triandrum* E.M. Marais, has four petals, and *P. leipoldtii*, *P. ellaphieae*, *P. asarifolium*, *P. dipetalum*, and *P. ternifolium* have flowers with only two petals each in the posterior position. The androeciums of the two-petalled flowers are very similar and the reduction in the number of petals confirms the relationships among these species.

The shape and size of the petals are important characters used in the taxonomic treatment of the section. The posterior petals are always longer and wider than the anterior ones, except in *P. pilosellifolium* and *P. fumariifolium*, where the anterior petals are longer than the posterior ones. These two species are not closely related because *P. pilosellifolium* has very short stamens and *P. fumariifolium* has longer stamens which are twisted in an unusual way. In *P. luteum* the posterior petals and anterior ones have more or less the same length. This is also true for *P. luteolum*, although in the latter the

anterior petals are wider than the posterior ones. The anterior petals of *P. luteolum* are also borne in a special way; the median one is covered by the lateral two, enclosing the stamens at the same time. The same orientation of the anterior petals is found in *P. gracillimum*. The papilionaceous flowers of *P. rapaceum* is a unique type of floral structure for *Pelargonium*. The anterior petal is very wide (5--11 mm) and conduplicate like the keel of a papilionaceous type of flower, enclosing the relatively long and straight stamens. The two lateral petals or wings cover the keel. The two posterior petals are unguiculate-spathulate and bend backwards above the claws.

The length (Table 3.4) and the length/width ratio (Table 3.4) of the posterior petals play an important role in the delimitation of the different floral structure groups. Some species with very short stamens have long ligulate petals, with a length/width ratio bigger than five (*P. attenuatum* Harv., *P. angustipetalum* E.M. Marais, *P. leptum* L. Bol., *P. viciifolium* DC., *P. longifolium*, *P. fergusoniae* L. Bol., *P. undulatum* (Andr.) Pers., *P. longiflorum* and *P. aristatum* (Sweet) G. Don), whereas others have shorter, but wider petals with a length/width ratio of less than five (*P. chelidonium*, *P. nervifolium* Jacq., *P. pinnatum*, *P. reflexum* (Andr.) Pers., *P. violiflorum* (Sweet) DC., *P. aestivale*, *P. fissifolium* and *P. petroselinifolium*).

Table 3.4 The length/width ratio and the length of the posterior petals of the species of section *Hoarea*.

Species	Length/width		Length (mm)				
	0	10	0	10	20	30	40
<i>P. aestivale</i>							
<i>P. fissifolium</i>							
<i>P. petroselinifolium</i>							
<i>P. aristatum</i>							
<i>P. chelidonium</i>							
<i>P. nervifolium</i>							
<i>P. pinnatum</i>							
<i>P. reflexum</i>							
<i>P. violiflorum</i>							
<i>P. attenuatum</i>							
<i>P. angustipetalum</i>							
<i>P. leptum</i>							
<i>P. viciifolium</i>							
<i>P. longifolium</i>							
<i>P. fergusoniae</i>							
<i>P. undulatum</i>							
<i>P. longiflorum</i>							
<i>P. proliferum</i>							
<i>P. pilosellifolium</i>							
<i>P. caledonicum</i>							

Table 3.4 The length/width ratio and the length of the posterior petals of the species of section *Hoarea* (continue).

Species	Length/width		Length (mm)				
	0	10	0	10	20	30	40
<i>P. heterophyllum</i>							
<i>P. tenellum</i>							
<i>P. trifoliolatum</i>							
<i>P. aciculatum</i>							
<i>P. confertum</i>							
<i>P. fasciculaceum</i>							
<i>P. connivens</i>							
<i>P. luteum</i>							
<i>P. fumarifolium</i>							
<i>P. incrassatum</i>							
<i>P. grenvilleae</i>							
<i>P. moniliforme</i>							
<i>P. vinaceum</i>							
<i>P. radicatum</i>							
<i>P. appendiculatum</i>							
<i>P. campestre</i>							
<i>P. nephrophyllum</i>							
<i>P. carneum</i>							
<i>P. radiatum</i>							
<i>P. nummulifolium</i>							
<i>P. luteolum</i>							
<i>P. gracillimum</i>							
<i>P. rapaceum</i>							
<i>P. auritum</i> var. <i>auritum</i>							
<i>P. auritum</i> var. <i>carneum</i>							
<i>P. bubonifolium</i>							
<i>P. parvipetalum</i>							
<i>P. leipoldtii</i>							
<i>P. ellaphieae</i>							
<i>P. asarifolium</i>							
<i>P. dipetalum</i>							
<i>P. ternifolium</i>							
<i>P. triphyllum</i>							

Table 3.4 The length/width ratio and the length of the posterior petals of the species of section *Hoarea* (continue).

Species	Length/width		Length (mm)		
	0	10	20	30	40
<i>P. githagineum</i>	====	====			
<i>P. caroli-henrici</i>	====	====			
<i>P. rubiginosum</i>	====	====			
<i>P. oblongatum</i>	====			=====	
<i>P. curviandrum</i>	====	====	=====		
<i>P. triandrum</i>	====		=====		
<i>P. punctatum</i>	====	====	=====		

Several species have petals with undulate margins. In *P. heterophyllum*, *P. tenellum* (Andr.) G. Don and *P. trifoliolatum* this character confirms relationship. The undulate margins of the petals, together with an identical androecium confirms the relationship between *P. asarifolium* and *P. ellaphieae*.

Androecium

Different modifications of flowers, which include among others stamen number, stamen length, anther position, ovary position, style length, stigma shape, and size and form of perianth parts, contribute to the reproductive success of the species (Jones & Luchsinger 1987). They also stated that the value of characters drawn from reproductive morphology varies from group to group within the angiosperms. This is true for the evolutionary history of *Pelargonium*. In section *Hoarea* the modifications in the floral structure result in a large variation in the structure of the androecium, whereas the variation in the androecium of sections *Pelargonium*, *Otidia* (Sweet) DC. and *Myrrhidium* DC. is less prominent (Marais 1981).

The androecium of *Pelargonium* consists of ten filaments, arranged in two whorls of five each, basally connate, and obdiplostemonous (Figure 3.2). Usually the staminal column is smooth, but in *P. auritum*, *P. bubonifolium*, *P. parvipetalum* and all the two-petalled species it is papillate (Figure 3.3), a characteristic that suggests a relationship among these species. The androecium is zygomorphic; the staminal column is longer on the posterior side than on the anterior side and the anterior stamens are longer than the posterior one. In the genus *Pelargonium* the number of fertile stamens varies from two to seven and the staminodes are usually much shorter than the stamens. However, *P. fumariifolium* has very long staminodes, which are not only unique for *Hoarea*, but also unique for the genus, and therefore a diagnostic feature for this species. In Figure 3.2

the stamens are numbered clockwise with the posterior stamen as no. 1, and in Table 3.5 the positions of the fertile stamens for the genus are given. From this it is clear that in section *Hoarea* the filaments of the outer whorl are always lacking anthers. At the same time the variation in the different filaments of the inner whorl which bear anthers, is also revealed. The number of fertile stamens is rather a diagnostic feature than one to establish interrelationships in the section.

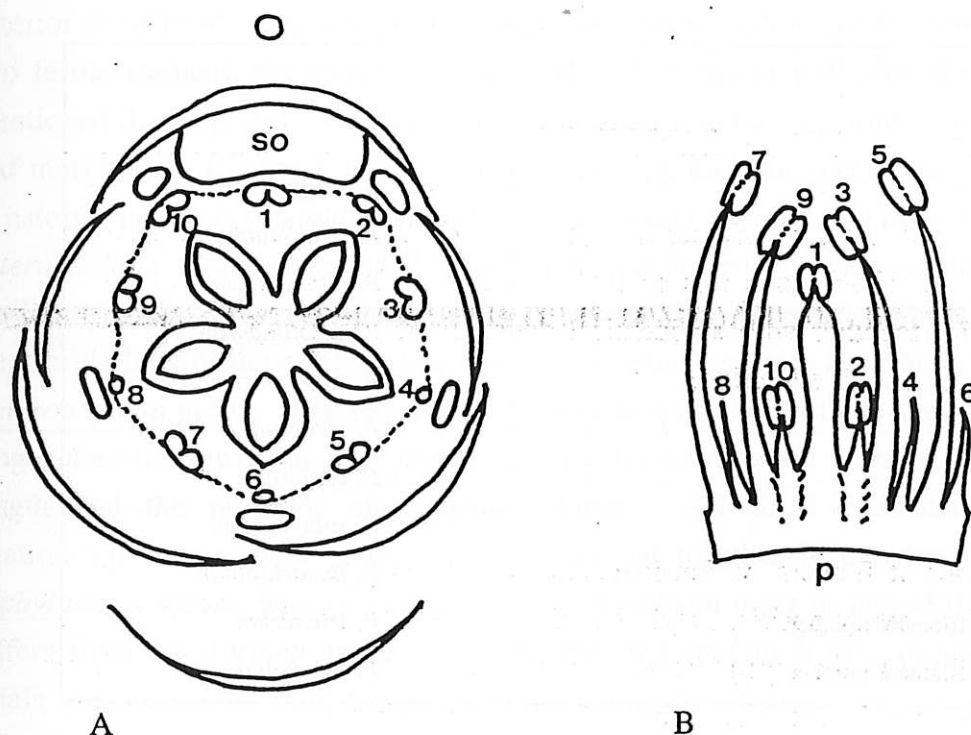


Figure 3.2 A, Floral diagram of *Pelargonium* to illustrate the position of the stamens. B, The androecium of *Pelargonium*. p = posterior, so = spur opening.

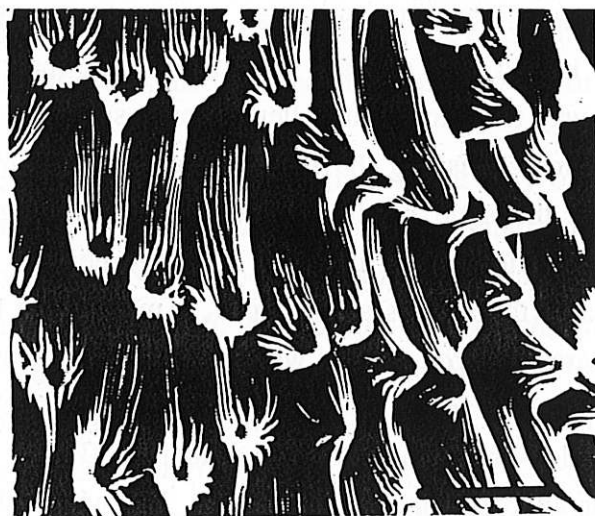


Figure 3.3 Scanning electron micrograph of the papillate staminal column of *P. auritum* var. *auritum* (Van der Walt 482). Scale bar: 50 μ m.

Table 3.5 The androecium of *Pelargonium*, illustrating the position of the fertile stamens

Number of fertile stamens	Stamens with anthers, numbered according to Figure 3.3.										
	7	8	9	10	1	2	3	4	5	6	Outer whorl Inner whorl
7	*	-	*	*	*	*	*	-	*	-	
6	*	-	*	*	-	*	*	-	*	-	

Section <i>Hoarea</i>											
5	*	-	*	-	*	-	*	-	*	-	
4	*	-	*	-	-	-	*	-	*	-	<i>P. longiflorum</i>
											<i>P. ternifolium</i>
											<i>P. githagineum</i>
											<i>P. caroli-henrici</i>
											<i>P. curviandrum</i>
2,3,4	*	-	?	-	-	-	?	-	*	-	<i>P. vinaceum</i>
2	*	-	-	-	-	-	-	-	*	-	<i>P. confertum</i>
											<i>P. rubiginosum</i>
2	-	-	*	-	-	-	*	-	-	-	<i>P. fumariifolium</i>
3	Reduction in filament number										<i>P. triandrum</i>
2	Reduction in filament number										<i>P. punctatum</i>

All the species in section *Hoarea* share more or less the same basic structure of the androecium, the posterior stamen is short, the lateral two somewhat longer and the anterior two the longest. The posterior and lateral stamens are twisted in such a way that the dehiscent anthers show backwards. The flowers of all the species in this section are protandrous. When the petals unfold, the stamens are longer than the pistil and the dehiscent anthers are borne in a way to form a flat pollen-covered surface which must be touched by the abdomen of the insect visiting the flowers (Scott Elliot 1891). During anthesis the pistil lengthens and the style bends upwards, while the stigma branches recurve, occupying the original position of the anthers. At the same time the filaments bend downwards and in most cases the anthers are dropped, a mechanism to avoid self-pollination. Exceptions to this are *P. caroli-henrici* where the free filaments are twisted so that pollen surfaces are turned to the front, *P. luteum* where the filaments are twisted in a unique way, forming a pollen-lined tunnel to the nectar tube (Figure 8.28.2), and *P. fumariifolium* with a similar androecium than *P. luteum*, but with only two fertile stamens.

The relative length of the stamens is diagnostic at specific level and varies from much shorter than, the same length as, or longer than the calyx (Table 3.3). The comparison of the stamen length to that of the sepals is a practical one, since the sepals are persistent and the comparison is still possible, even after the petals are dropped. The differences in the length between the posterior stamen, the lateral stamens, and the anterior stamens vary in the different species. In *P. aciculatum*, *P. fasciculaceum* and *P. connivens* the posterior and lateral stamens are very short and concealed within the floral sheath. The anterior stamens are long and protrude from the flower. Although *P. confertum* has only two fertile stamens, the structure of the androecium fits in well with that of the above mentioned three species. Because of the resemblance in the structure of the androecium, leaf morphology (Figure 3.1) and pollen structure, these four species can be regarded as a natural taxon (*Aciculatum* group) within section *Hoarea* (Marais 1991). In *P. heterophyllum*, *P. tenellum* and *P. trifoliolatum* the posterior stamen is much shorter than the lateral and the anterior ones, and in respect to this character, and the similarities in the morphology of the petals and the pollen, these three species are placed together as the *Heterophyllum* group. The stamens of the species with the papillate staminal column are longer than the sepals, and the lateral and anterior stamens are more or less of the same length and the posterior one slightly shorter. All these characters confirm the relationship among these species and they are put together in the *Auratum* group. *P. triphyllum*, a species with five long stamens, all of them more or less of the same length, differs from the *Auratum* group in that the staminal column is smooth and the posterior petals are auriculate, thus forming a floral group of its own (*Triphyllum* group). In several species the stamens are long and straight and an obvious difference occurs in the lengths of the posterior, lateral and anterior stamens (*Incrassatum*, *Luteolum* and *Rapaceum* groups). The *Luteolum* group is distinguished in respect to the wide anterior petals and the way the anterior petals enclose the stamens, and the *Rapaceum* group is distinguished in respect to the papilionaceous type of corolla. The *Luteum* group (*P. luteum* and *P. fumariifolium*) is distinguished in respect to the orientation of the stamens.

The variation in the structure of the androecium is not only of diagnostic value, but it is also the most important character set to delimit smaller taxonomic units within the section. In about one third of the species studied, the stamens are short and concealed within the floral sheath (Table 3.6: *Fissifolium*, *Pinnatum*, *Attenuatum* and *Proliferum* groups). In another third the anterior stamens are more or less the same length as the sepals and depending on the orientation of the petals, the stamens sometimes protrude from the flower (Table 3.6: *Heterophyllum*, *Aciculatum*, *Luteum*, *Incrassatum*, *Luteolum* and *Rapaceum* groups). In the rest of the species the stamens are long and protrude from the flower (Table 3.6: *Auratum*, *Triphyllum*, *Caroli-henrici* and *Punctatum* groups). Both

the *Caroli-henrici* and *Punctatum* groups have long stamens. They differ because in the *Punctatum* group the stamens are very long and curved upwards, whereas those of the *Caroli-henrici* group remain straight during anthesis.

In respect to the length of the different stamens and the ratio between the length of the stamens and that of the sepals or petals, different types of floral structures are recognized (Table 3.6). The size and the form of the petals (*Pinnatum* group with spatulate petals, and *Attenuatum* group with ligulate petals) and the structure of the pollen (*Proliferum* group) also play a major role in constructing the different floral structure groups. In Table 3.6 species are listed according to the different floral groups, and at the same time, the different leaf forms, as defined in Figure 3.1 are included.

Table 3.6 Different floral groups of section *Hoarea* and the different leaf forms occurring in each group.

Floral group / species	Leaf forms as defined in Figure 3.1											
	1	2	3	4	5	6	7	8	9	10	11	12
1.Fissifolium group												
<i>P. aestivale</i>		*										
<i>P. fissifolium</i>											*	
<i>P. petroselinifolium</i>											*	
<i>P. aristatum</i>											*	
2.Pinnatum group												
<i>P. chelidonium</i>		*										
<i>P. nervifolium</i>		*										
<i>P. pinnatum</i>									*			
<i>P. reflexum</i>				*								
<i>P. violiflorum</i>										*		
3.Attenuatum group												
<i>P. attenuatum</i>					*							
<i>P. angustipetalum</i>					*							
<i>P. leptum</i>										*		
<i>P. viciifolium</i>									*			
<i>P. longifolium</i>											*	
<i>P. fergusoniae</i>				*					*			
<i>P. undulatum</i>									*			
<i>P. longiflorum</i>									*			
4.Proliferum group												
<i>P. proliferum</i>						*						
<i>P. pilosellifolium</i>							*					
<i>P. caledonicum</i>											*	
5.Heterophyllum group												
<i>P. heterophyllum</i>		*										
<i>P. tenellum</i>		*										
<i>P. trifoliolatum</i>									*			

Table 3.6 Different floral groups of section *Hoarea* and the different leaf forms occurring in each group (continue).

Floral group / species	Leaf forms as defined in Figure 3.1											
	1	2	3	4	5	6	7	8	9	10	11	12
14. Punctatum group												
<i>P. oblongatum</i>	*											
<i>P. curviandrum</i>	*											
<i>P. triandrum</i>	*											
<i>P. punctatum</i>	*											

Key to Table 3.6

1. Simple, cordiform, prostrate
2. Simple (ovate to cordiform) to tripartite or trifoliolate, prostrate
3. Simple (palmately veined), reniform, petiole curved
4. Palmately compound, ternate to tripinnatisect, petiole curved
5. Palmately compound, ternate to tripinnatisect, petiole erect
6. Simple to tripartite or trifoliolate, lanceolate, petiole erect
7. Simple to pinnatisect or pinnately compound, lanceolate, petiole erect
8. Simple or pinnately compound to irregularly bipinnatisect, lanceolate to ovate, petiole erect
9. Pinnately compound, erect, pinnate
10. Pinnately compound, erect, pinnatisect to pinnate, trullate or elliptic
11. Pinnately compound, erect, pinnate to irregularly bi- or tripinnatisect
12. Pinnately compound, erect, irregularly bi- or tripinnatisect, aciculatum group

Gynoecium

The gynoecium in section *Hoarea* is typical for *Pelargonium*, consisting of a densely sericeous, four- or five-lobed, oblong-conical ovary, a filiform style and a stigma with four or five recurved branches. In *P. punctatum* (Andr.) Willd., *P. triandrum* and *P. rubiginosum* the stigma branches are very short and incapable of recurving. The ovary consists of a basal part containing the ovules and a rostrum which lengthens greatly after fertilization. The flowers of *Hoarea* are protandrous and when the petals unfold the pistil is much shorter than the stamens, except in *P. githagineum*, where closed stigma branches protrude from the flower bud. During anthesis the rostrum, style and often the stigma branches lengthen, and when the stamens bend down and the anthers are dropped, the recurved stigma branches take the original position of the anthers. This causes a large variation in the measurements of the pistil, as a result the measurements are less useful for diagnostic purposes. Species with long stamens also have long styles.

Fruit

The fruit is typical for the Geraniaceae. It is a schizocarp with five mericarps, with the exception of *P. punctatum* and *P. triandrum* which usually have only four mericarps.

When ripe, the four or five mericarps, each with an enclosed seed, are distributed by the wind. The length of the base varies from (3-)4--6(-8) mm, and that of the rostrum from (13-)18--37(-55) mm. *P. appendiculatum* has the longest fruits (rostrum is 50--55 mm long) and those of *P. nephrophyllum* are the shortest (rostrum is 13--17 mm long). The presence or absence of glandular hairs on the distal side of the base (Figure 3.4) could be of diagnostic value at species level (Table 3.7).

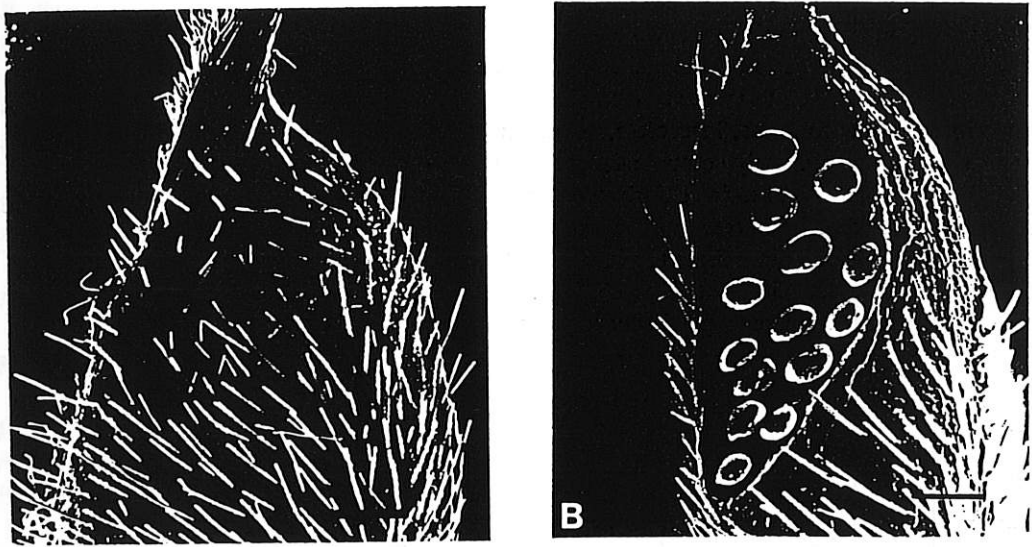


Figure 3.4 The distal side of the fruit base. A, without glandular hairs of *P. trifoliolatum* (Marais 178) and B, with glandular hairs of *P. radiatum* (Van der Walt 970). Scale bar: 0,25 mm.

Table 3.7 The length of the fruit of the different *Hoarea* species and the presence of glandular hairs on the base

Species	Gla	Base length	Rostrum length			
			0	20	40	mm
1. Fissifolium group						
<i>P. aestivale</i>	*	—			—	
<i>P. fissifolium</i>	*	—		—		
<i>P. petroselinifolium</i>	*	—		—		
<i>P. aristatum</i>	*	—		—		
2. Pinnatum group						
<i>P. chelidonium</i>	*	—		—		
<i>P. nervifolium</i>	*	—		—		
<i>P. pinnatum</i>	-	—		—		
<i>P. reflexum</i>	*	—		—		
<i>P. violiflorum</i>	-	—		—		

Table 3.7 The length of the fruit of the different *Hoarea* species and the presence of glandular hairs on the base (continue).

Species	Gla	Base length	Rostrum length			
			0	20	40	mm
3. Attenuatum group						
<i>P. attenuatum</i>	*	—		—		
<i>P. angustipetalum</i>	*	—		—		
<i>P. leptum</i>	-	—		—		
<i>P. viciifolium</i>	*	—		—		
<i>P. longifolium</i>	-	—			—	
<i>P. fergusoniae</i>	-	—		—		
<i>P. undulatum</i>	*	—			—	
<i>P. longiflorum</i>	-	—				—
4. Proliferum group						
<i>P. proliferum</i>	-	—		—		
<i>P. pilosellifolium</i>	-	—			—	
<i>P. caledonicum</i>	-	—		—		
5. Heterophyllum group						
<i>P. heterophyllum</i>	?	—				
<i>P. tenellum</i>	?	—				
<i>P. trifoliolatum</i>	-	—		—		
6. Aciculatum group						
<i>P. aciculatum</i>	*	—		—		
<i>P. confertum</i>	*	—		—		
<i>P. fasciculaceum</i>	?	—		—		
<i>P. connivens</i>	?	—		—		
7. Luteum group						
<i>P. luteum</i>	*	—		—		
<i>P. fumarifolium</i>	*	—		—		
8. Incrassatum group						
<i>P. incrassatum</i>	-	—			—	
<i>P. grenvilleae</i>	?	—				
<i>P. moniliforme</i>	-	—		—		
<i>P. vinaceum</i>	-	—		—		
<i>P. radicatum</i>	*	—			—	
<i>P. appendiculatum</i>	-	—				—
<i>P. campestre</i>	*	—		—		
<i>P. nephrophyllum</i>	*	—		—		
<i>P. carneum</i>	*	—		—		
<i>P. radiatum</i>	*	—		—		
<i>P. nummulifolium</i>	*	—		—		
9. Luteolum group						
<i>P. luteolum</i>	*	—		—		
<i>P. gracillimum</i>	*	—		—		

Table 3.7 The length of the fruit of the different *Hoarea* species and the presence of glandular hairs on the base (continue)

Species	Gla	Base length	Rostrum length			mm
			0	20	40	
10. Rapaceum group						
<i>P. rapaceum</i>	*	—		—————		
11. Auritum group						
<i>P. auritum</i> var. <i>auritum</i>	*	—		—————		
<i>P. auritum</i> var. <i>carneum</i>	-					
<i>P. bubonifolium</i>	*	—		—————		
<i>P. parvipetalum</i>	*	—		—————		
<i>P. leipoldtii</i>	*	—			—————	
<i>P. ellaphieae</i>	*	—				—————
<i>P. asarifolium</i>	-	—		—————		
<i>P. dipetalum</i>	-	—		—————		
<i>P. ternifolium</i>	-	—		—————		
12. Triphyllum group						
<i>P. triphyllum</i>	*	—		—————		
13. Caroli-henrici group						
<i>P. githagineum</i>	-	—			—————	
<i>P. caroli-henrici</i>	-	—			—————	
<i>P. rubiginosum</i>	-	—		—————		
14. Punctatum group						
<i>P. oblongatum</i>	*	—			—————	
<i>P. curviandrum</i>	*	—		—————		
<i>P. triandrum</i>	-	—		—————		
<i>P. punctatum</i>	-	—		—————		

gla, * = glandular hairs; - = without glandular hairs; ? = not seen

Discussion

Natural selection, associated with successful reproduction, maintains a basic similarity of the reproductive features of flowers within the various species. This general constancy makes these structures ideal for characterizing taxonomic groups. Floral features are often fundamental in defining natural groups (Jones & Luchsinger 1987). In section *Hoarea* the characteristics of the androecium have proved to be most useful in the classification of the section. The relative length of the stamens can be used to distinguish between species, but can also confirm interrelationships among species. This includes the length of the stamens if compared to that of the sepals and the differences in the length of the posterior, lateral and anterior stamens. In about one third of the species the stamens are shorter than the sepals (*Fissifolium*, *Pinnatum*, *Attenuatum* and *Proliferum* groups). The ratios between the length of the posterior and lateral stamens, and that of the lateral

and the anterior ones in these species, are more or less the same (Table 3.3). All these species have less than 20 flowers per pseudo-umbellet (Table 3.1). If the length and the length/width ratio of the posterior petals of these species are considered, they can be divided into smaller groups. The *Pinnatum* group has flowers with spatulate petals, of which the length/width ratio of the posterior petals is smaller than five, and the *Attenuatum* group has long ligulate petals with a length/width ratio of bigger than five. Because of the petal size and the uniformity of the pollen structure, *P. proliferum*, *P. pilosellifolium* and *P. caledonicum* are placed in the *Proliferum* group. The differences in the length of the posterior, lateral and anterior stamens demarcate the *Aciculatum*, *Heterophyllum* and *Incrassatum* groups. In respect to petal size, length/width ratio of the posterior petals, hypanthium length, and flower number per pseudo-umbellet the *Incrassatum* group can be subdivided into smaller groups. The papilionaceous flower of *P. rapaceum* is a unique type of floral structure and demarcates this species as a monotypic group. The delimitation of the *Luteolum* group (*P. luteolum* and *P. gracillimum*) is based on the way the anterior petals are borne during anthesis, and leaf shape supports this demarcation.

In *P. luteum* and *P. fumariifolium* the stamens are twisted in a similar way, with open anthers facing to the front. Both species have the same petal morphology, nectar guides, hypanthium length, inflorescence size and in both species the flowers have the same delicate appearance, forming the *Luteum* floral group.

The outstanding characters of the *Auratum* group are long stamens, all of them of the same length, and the papillate staminal column. *P. triphyllum* has the same long stamens as the *Auratum* group, but the staminal column is smooth, forming a floral group of its own (*Triphyllum* group).

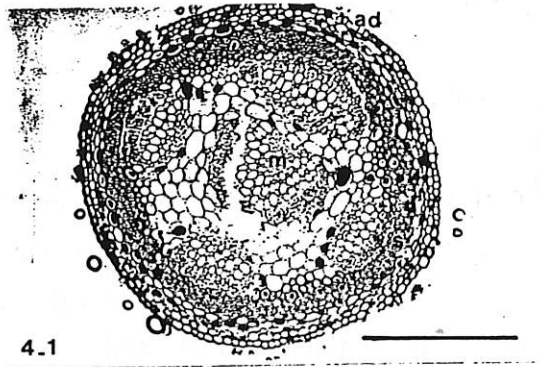
Although the division of section *Hoarea* is mainly based on the variations in the androecium and petals, several other characters also play a role in the demarcation of the different groups. There is no single character that confirms relationship in all the groups. Most of the characters confirm relationships in some groups, but at the same time act as a diagnostic tool in other groups. None of the groups can be demarcated by only one character, in all of them a combination of characters is necessary for the delimitation.

CHAPTER 4

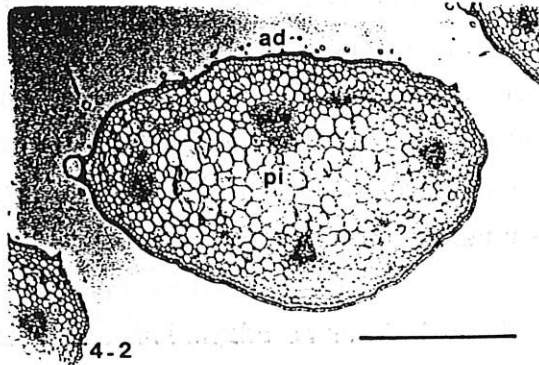
LEAF ANATOMY

Anatomical characters can be taxonomically useful as an aid toward establishing the interrelationships of taxa at and above the species level. Like all other taxonomic characters, a distinction must be made between diagnostic taxonomic characters that can be used to distinguish between different taxa, or characters that assist in our understanding the evolutionary relationships of plants (Dickison 1975). Several taxonomists applied leaf anatomical data for these purposes in the Geraniaceae. In *Sarcocaulon* (DC.) Sweet the anatomy of the lamina confirms the demarcation of two of the sections and with lamina anatomy in combination with trichomes all four sections of the genus can be distinguished (Verhoeven *et al.* 1983a, 1983b). Neubauer (1972) regarded the presence or absence of a medullary bundle in the petiole of *Pelargonium* as of taxonomic value, a point of view which was confirmed for sections *Pelargonium* (Volschenk, 1980), *Myrrhidium* DC. (Van der Walt & Boucher 1986), *Polyactium* DC. (Maggs 1987), *Campylia* (Sweet) DC. (Van der Walt & Van Zyl 1988), *Jenkinsonia* (Sweet) Harv. (Scheltema & Van der Walt 1990), and *Ligularia* (Sweet) Harv. (Marais 1990b). In *Polyactium* (Maggs 1987) and *Hoarea* (Marais 1991) the structure of the medullary bundle varies from a single bundle, consisting of one to three fused bundles, to several bundles. This may probably be ascribed to the way in which the medullary bundles are formed as described by Neubauer (1972), Volschenk (1980), and Dreyer (1990b). According to Dreyer (1990b) and Dreyer *et al.* (1992) petiole anatomy strengthens the evidence for the demarcation of the section *Reniformia* (Knuth) Dreyer and section *Cortusina* (DC.) Harv. *sensu stricto*. The presence of perivascular sclerenchymatous tissue in the petiole varies from sclerenchyma strands, restricted to the vascular bundles (Van der Walt & Van Zyl 1988, Dreyer 1990b, Marais 1990b), to a continuous cylinder as in *Myrrhidium* (Van der Walt & Boucher 1986), *Campylia* (Van der Walt & Van Zyl 1988), *Reniformia* (Dreyer 1990b), and *Hoarea* (Marais 1991). Both dorsiventral and isobilateral leaves occur in sections *Pelargonium* (Volschenk 1980), *Myrrhidium* (Van der Walt & Boucher 1986), *Campylia* (Van der Walt & Van Zyl 1988), *Jenkinsonia* (Scheltema & Van der Walt 1990), *Ligularia* (Marais 1990b), *Cortusina sensu stricto* and *Reniformia* (Dreyer 1990b), and often closely related taxa can be distinguished because of the dorsiventral or isobilateral leaves.

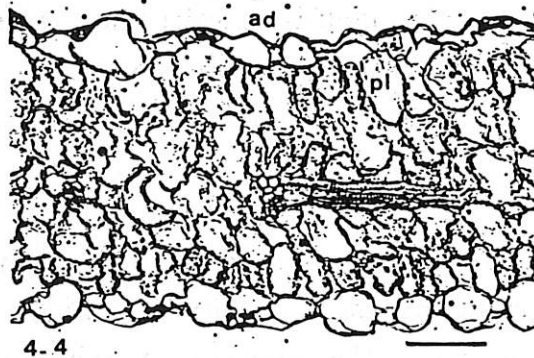
According to Dickison (1975) it is essential that the ranges of variability of anatomical characters within the same individual and different individuals in relation to the environment should be investigated. Carlquist (1961) stressed the need to describe the



4.1



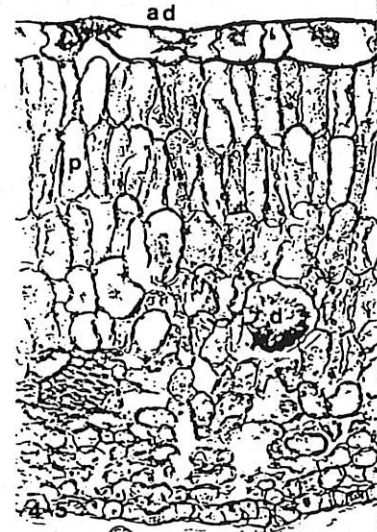
4.2



4.4



4.3



4.5

Figure 4.1 Transverse section of the petiole of *P. luteolum* (Lavranos 20266). Scale bar: 0,3 mm.

Figure 4.2 Transverse section of the petiole of *P. tenellum* (Van der Walt 1027). Scale bar: 0,65 mm.

Figure 4.3 Transverse section of the lamina of *P. githagineum* (Lavranos 20785a). Scale bar: 60 μ m.

Figure 4.4 Transverse section of the lamina of *P. rubiginosum* (Van Jaarsveld 4100). Scale bar: 60 μ m.

Figure 4.5 Transverse section of the lamina of *P. asarifolium* (Van der Walt 1062). Scale bar: 60 μ m.

ad = adaxial, d = druse, m = medullary vascular bundle, p = palisade, pi = pith, pl = palisade-like, s = schlerenchyma cylinder.

entire range of character variation of a given tissue or structure. For this reason an average of three specimens per species were studied where material was available (Table 4.7). The material studied was from plants growing for more than one season in the Botanic Garden of the University of Stellenbosch. This ensures that all the material studied was from plants growing for a considerable time under similar environmental conditions, and thus excluding to a large extent variations that could be ascribed to ecological factors.

According to Stuessy (1990) the leaf outline and the internal architecture of the leaf could be of taxonomic importance. Because of the variation in leaf form in section *Hoarea*, the leaf outline could be of taxonomic value in some cases, but because of the heteroblastic leaf development in many species this is not always a reliable taxonomic character in this section. Additional to leaf form the internal architecture was studied for diagnostic characters as well as characters to confirm relationships between species.

The anatomy of the leaves of section *Hoarea* shows little or no adaptations to the xeric habitats in which most of the species occur. All the species are deciduous geophytes, shedding their leaves during the summer and the habitus itself is an adaptation to survive the unfavourable season.

Anatomy of the petiole

The transverse sections of the middle part of the petioles of the different species vary from round, adaxially flattened or slightly grooved. In all species the petioles are covered by a uniseriate epidermis with different combinations of glandular hairs and/or non-glandular hairs. The cortex comprises a uniseriate collenchymatous hypodermis and two to six layers of chlorenchyma cells. The vascular tissue consists of a cylinder of four main bundles alternating with a varying number of medium-sized and smaller bundles. In very thin petioles as in *P. angustipetalum*, *P. fergusoniae*, *P. luteolum* (Figure 4.1) and *P. gracillimum* only four large bundles occur in the cylinder. In all the studied species, except *P. tenellum* (Figure 4.2) a medullary bundle occurs, consisting of one to three fused bundles. This medullary bundle is often in association with the adaxial bundle (Marais 1993). In some species more than one medullary bundle occur (Marais 1991), but the number is not consistent for a species. The presence of perivascular sclerenchymatous tissue varies. In species with prostrate leaves it is usually lacking in the median section, but can be present at the proximal end (Marais 1992). In species with erecto-patent leaves the sclerenchyma is restricted to strands on the outside of the vascular bundles. In these cases there is sometimes a tendency towards a continuous

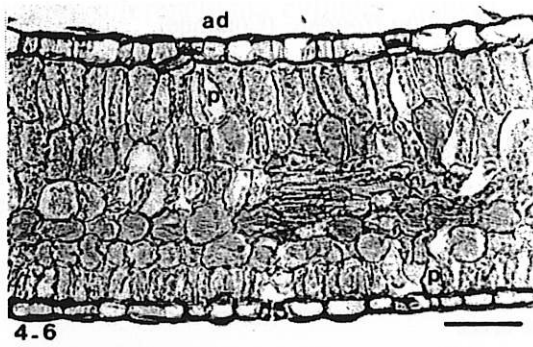
sclerenchymatous cylinder surrounding the vascular bundles. In rigid erect petioles a perivascular sclerenchyma cylinder, consisting of three to six cell layers occurs (Marais 1991, Marais 1993), and in the very thin petioles of *P. angustipetalum*, *P. fergusoniae*, *P. reflexum*, *P. luteolum* and *P. gracillimum* this cylinder is very prominent (Figure 4.1). In these species the chlorenchyma tissue surrounding the sclerenchyma consists of only two cell layers. In all species the pith consists of rather large parenchyma cells.

Table 4.1 Leaf anatomical characters in the different leaf forms of section *Hoarea*. (Species arranged according to leaf form.)

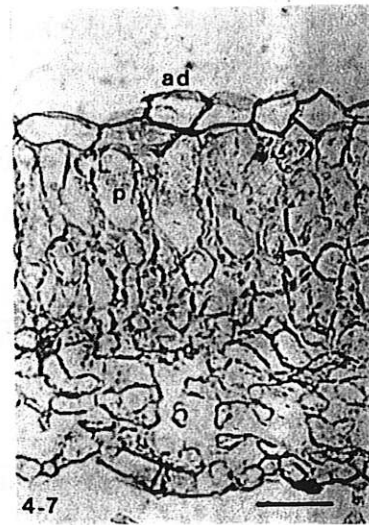
Leaf form / species	1	2	3	4	5	6	7	8	9
1. Simple, cordiform, prostrate									
<i>P. punctatum</i>	*		2-3		L			*	
<i>P. triandrum</i>	*		1		L	B		*	
<i>P. curviandrum</i>	*		2-3			B		*	
<i>P. oblongatum</i>	*		2		L			*	
<i>P. githagineum</i>	*		2		L	B		*	
<i>P. asarifolium</i>	*		3-4		L				*
2. Simple (ovate to cordiform) to tripartite or trifoliolate, prostrate									
<i>P. moniliforme</i>	*		2		L	B		*	
<i>P. vinaceum</i>	*		2		L			*	
<i>P. nervifolium</i>	*		3-4		L		*	*	
<i>P. triphyllum</i>	*		2-3		L			*	
<i>P. campestre</i>									
<i>P. aestivale</i>	*		2-3		M	B		*	
<i>P. heterophyllum</i>	*		3		L				*
<i>P. tenellum</i>	*		2-4		L				*
<i>P. chelidonium</i>									
<i>P. grenvilleae</i>	*		2-3		L	B	?		*
<i>P. radiatum</i>	*		2-3		L				*
<i>P. nummulifolium</i>	*		2-3		L				*
3. Simple (palmately veined), reniform, petiole curved									
<i>P. nephrophyllum</i>	*		2		M	B		*	
4. Palmately compound, ternate to tripinnatisect, petiole curved									
<i>P. ternifolium</i>	*		1-2		M	B	*	*	
<i>P. reflexum</i>		*	2	1	M	B			*
<i>P. fergusoniae</i>	*		2		S	B			*
1.	Leaves dorsiventral								
2.	Leaves isobilateral								
3.	Number of palisade layers adaxially								
4.	Number of palisade layers abaxially								
5.	Palisade cells short (S), medium length (M), long (L)								
6.	Palisade cells broad (B)								
7.	Stained layer								
8.	Spongy tissue loosely arranged								
9.	Mesophyll compact								

Table 4.1 Leaf anatomical characters in the different leaf forms of section *Hoarea*. (Continue)

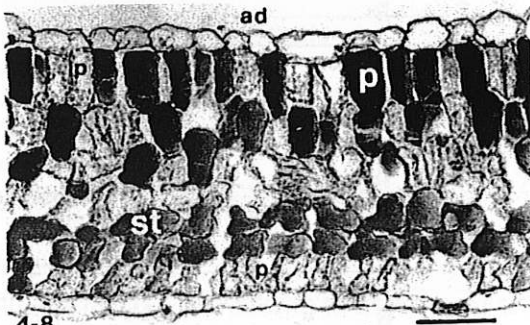
Leaf form / species	1	2	3	4	5	6	7	8	9
5. Palmately compound, ternate to tripinnatisect, petiole erect									
<i>P. luteolum</i>	*		2		S	B	*		*
<i>P. gracillimum</i>		*	2	1	S	B			*
<i>P. attenuatum</i>									
<i>P. angustipetalum</i>	*		2		S	B	*	*	
6. Simple to tripartite or trifoliolate, lanceolate, petiole erect									
<i>P. longiflorum</i>		*	2	1	S/L		*		*
<i>P. radicum</i>	*		2		S	B			*
<i>P. ellaphieae</i>	*		2		S	B			*
7. Simple to pinnatisect or pinnately compound, lanceolate, petiole erect									
<i>P. pilosellifolium</i>		*	2	1	M	B	?		*
8. Simple or pinnately compound to irregularly bipinnatisect, lanceolate to ovate, petiole erect									
<i>P. longifolium</i>		*	1-2	1	S	B	*		*
<i>P. proliferum</i>									
<i>P. dipetalum</i>		*	2	1	L		*		*
9. Pinnately compound, erect, pinnate									
<i>P. pinnatum</i>	*	*	1	1	M	B	*		*
<i>P. viciifolium</i>	*		1		M	B	*		*
<i>P. trifoliolatum</i>		*	1	1	M	B	*		*
10. Pinnately compound, erect, pinnatisect to pinnate, trullate or elliptic									
<i>P. leptum</i>		*	2	1	S		?		*
<i>P. undulatum</i>		*	2	1-2	S/L		?		*
<i>P. leipoldtii</i>	*	*	2	1	S/L	B	?		*
<i>P. fumariifolium</i>	*		2		S		*	*	
<i>P. violiflorum</i>	*		2-3		M	B		*	
11. Pinnately compound, erect, pinnate to irregularly bi- or tripinnatisect									
<i>P. auritum</i>		*	2	1	S				*
<i>P. incrassatum</i>		*	2	1	S/L		*		*
<i>P. fissifolium</i>		*	2	1	S				*
<i>P. petroselinifolium</i>		*	2	1	S				*
<i>P. aristatum</i>	*	*	2	1	S				*
<i>P. carneum</i>		*	2-3	1-2	M		*		*
<i>P. luteum</i>	*		2-3		L			*	
<i>P. bubonifolium</i>		*	2	1	M	B			*
<i>P. parvipetalum</i>		*	2	1	S	B	?		*
<i>P. appendiculatum</i>	*		1		S	B			*
<i>P. caroli-henrici</i>	*		2		S	B			*
<i>P. rubiginosum</i>	*		2		S	B			*
<i>P. caledonicum</i>									
<i>P. rapaceum</i>		*	2	1	M	B			*
12. Pinnately compound, erect, irregularly bi- or tripinnatisect, aciculatum group									
<i>P. aciculatum</i>	*		1		M	B			*
<i>P. confertum</i>	*		1		M	B			*
<i>P. fasciculaceum</i>	*		1		M	B			*
<i>P. connivens</i>	*		1		M	B			*



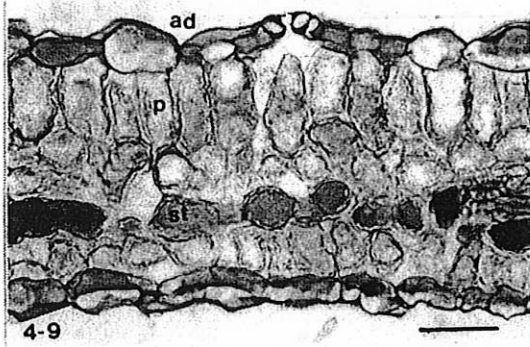
4-6



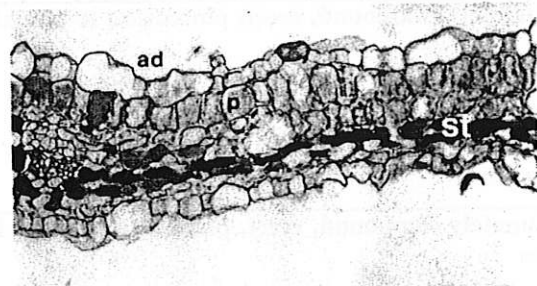
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Figure 4.6 Transverse section of the lamina of *P. pilosellifolium* (Fischer 293). Scale bar: 60 μm .

Figure 4.7 Transverse section of the lamina of *P. curviandrum* (Lavranos 20941). Scale bar: 60 μm .

Figure 4.8 Transverse section of the lamina of *P. undulatum* (Marais 331). Scale bar: 60 μm .

Figure 4.9 Transverse section of the lamina of *P. viciifolium* (Marais 13). Scale bar: 60 μm .

Figure 4.10 Transverse section of the lamina of *P. ternifolium* (Marais 319). Scale bar: 60 μm .

ad = adaxial, p = palisade, st = stained layer.

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Anatomy of the lamina

The laminae are amphistomatic with a uniserial epidermis and different combinations of glandular and non-glandular hairs, covered by a thin and smooth cuticle. Studies with the scanning electron microscope (SEM) of the leaves show that the cuticular wax patterns are of no taxonomic significance in section *Hoarea*. The cells of the adaxial epidermis are usually slightly larger than those of the abaxial side. However, in species with simple leaves like *P. githagineum* (Figure 4.3), *P. curviandrum* E.M. Marais, *P. nephrophyllum*, *P. vinaceum*, *P. asarifolium*, and *P. radicum* the difference is much more prominent. The abaxial epidermal cells of *P. nephrophyllum* and of *P. nervifolium* contain anthocyanin, hence the reddish purple colour on the lower side of the leaves. In surface view the anticlinal walls of the epidermis cells on both sides are sinuous.

In the majority of species (34) the laminae are dorsiventral, and in 18 species the leaves are isobilateral (Table 4.1). This is of diagnostic value, because environmental variations will not alter arrangements which are rigidly controlled by the genome (Cutler 1978). In *P. pinnatum*, *P. leipoldtii* and *P. aristatum* both leaf types occur (Table 4.1). The palisade cells in most species are rather broad (Figure 4.4, Table 4.1) and in *P. rubiginosum* (Figure 4.4), *P. caroli-henrici*, *P. radicum* and *P. appendiculatum* this tissue should rather be described as palisade-like. The number of palisade cell layers inside the adaxially epidermis varies from one to four, of which the outer layer consists of longer cells than the inner layers. In the case of *P. asarifolium* (Figure 4.5), *P. nervifolium* and *P. tenellum* the palisade tissue extends over half the cross section of the leaf. Although the number of palisade cell layers is a variable character which is easily influenced by environmental conditions (Cutler 1978), it must be kept in mind that the material studied here grew under similar conditions. In isobilateral leaves usually only one layer of palisade cells occurs inside the abaxial epidermis (Figure 4.6). In the majority of species (38) the mesophyll is rather compact with small and few air spaces (Table 4.1, Figure 4.6). This includes all the species with isobilateral leaves. Although it is not true for all species with simple or trifoliolate leaves, the majority of them have spongy tissue with large intercellular spaces (Table 4.1, Figure 4.7). Five species with compound leaves (*P. ternifolium*, *P. angustipetalum*, *P. fumariifolium*, *P. luteum* and *P. violiflorum*) have similar loosely arranged spongy parenchyma cells. In more or less one third of the species studied, a prominently stained layer of cells occurs on the abaxial side of the mesophyll (Marais 1993, Figures 4.8 & 4.9). In the isobilateral leaves this layer occurs on the inside of the abaxial palisade cells (Figure 4.8) and in the dorsiventral leaves this layer represents the second layer inside the abaxial epidermis (Figure 4.9). This layer is associated with the compact type of mesophyll, although it is not restricted

to this type of leaf (Table 4.1). Exceptions to this are *P. nervifolium*, *P. ternifolium* (Figure 4.10), *P. angustipetalum* and *P. fumarifolium*, all of them with a loosely arranged mesophyll. This stained layer does not always have the same intensity in the different specimens of the same species and is like-wise indicated (?) in Table 4.1.

The presence of idioblasts with tannin or druse crystals in the petioles and the laminae varies not only between species but also in different specimens of the same the species. Therefore I do not regard them as of any taxonomic value in section *Hoarea*. Druses in the petioles occur scattered through the pith, usually in the vicinity of the vascular bundles and in the laminae they occur on the border between the palisade and the spongy tissue or throughout the spongy tissue.

Table 4.2 Anatomical characters of the laminae compared to different leaf forms occurring in section *Hoarea*. (Species arranged according to leaf form)

Leaf form / species	1	2	3	4
1. Simple, cordiform, prostrate				
<i>P. punctatum</i>	■			
<i>P. triandrum</i>	■			
<i>P. curviandrum</i>	■			
<i>P. oblongatum</i>	■			
<i>P. githagineum</i>	■			
<i>P. asarifolium</i>		■		
2. Simple (ovate to cordiform) to tripartite or trifoliolate, prostrate				
<i>P. moniliforme</i>	■			
<i>P. vinaceum</i>	■			
<i>P. nervifolium</i>	■			■
<i>P. triphyllum</i>	■			
<i>P. campestre</i>				
<i>P. aestivale</i>	■			
<i>P. heterophyllum</i>		■		
<i>P. tenellum</i>		■		
<i>P. chelidonium</i>				
<i>P. grenvilleae</i>		■		■
<i>P. radiatum</i>		■		
<i>P. nummulifolium</i>		■		
3. Simple (palmately veined), reniform, petiole curved				
<i>P. nephrophyllum</i>	■			

1. Dorsiventral, spongy tissue loosely arranged
2. Dorsiventral, spongy tissue compact
3. Isobilateral, spongy tissue compact
4. Stained layer

Table 4.2 Anatomical characters of the laminae compared to different leaf forms occurring in section *Hoarea*. (Continue)

Leaf form / species	1	2	3	4
4. Palmately compound, ternate to tripinnatisect, petiole curved				
<i>P. ternifolium</i>	■			■
<i>P. reflexum</i>			■	
<i>P. fergusoniae</i>		■		
5. Palmately compound, ternate to tripinnatisect, petiole erect				
<i>P. luteolum</i>		■		■
<i>P. gracillimum</i>			■	
<i>P. attenuatum</i>				
<i>P. angustipetalum</i>	■			■
6. Simple to tripartite or trifoliolate, lanceolate, petiole erect				
<i>P. longiflorum</i>			■	■
<i>P. radicum</i>		■		
<i>P. ellaphieae</i>		■		
7. Simple to pinnatisect or pinnately compound, lanceolate, petiole erect				
<i>P. pilosellifolium</i>			■	■
8. Simple or pinnately compound to irregularly bipinnatisect, lanceolate to ovate, petiole erect				
<i>P. longifolium</i>			■	■
<i>P. proliferum</i>				
<i>P. dipetalum</i>			■	■
9. Pinnately compound, erect, pinnate				
<i>P. pinnatum</i>		■	■	■
<i>P. viciifolium</i>		■		■
<i>P. trifoliolatum</i>			■	■
10. Pinnately compound, erect, pinnatisect to pinnate, trullate or elliptic				
<i>P. leptum</i>			■	■
<i>P. undulatum</i>			■	■
<i>P. leipoldtii</i>		■	■	■
<i>P. fumariifolium</i>	■			■
<i>P. violiflorum</i>	■			
11. Pinnately compound, erect, pinnate to irregularly bi- or tripinnatisect				
<i>P. auritum</i>			■	
<i>P. incrassatum</i>			■	■
<i>P. fissifolium</i>			■	
<i>P. petroselinifolium</i>			■	
<i>P. aristatum</i>		■	■	
<i>P. luteum</i>	■			
<i>P. carneum</i>			■	■
<i>P. bubonifolium</i>			■	
<i>P. parvipetalum</i>			■	■
<i>P. appendiculatum</i>		■		
<i>P. caroli-henrici</i>		■		
<i>P. rubiginosum</i>		■		
<i>P. caledonicum</i>				
<i>P. rapaceum</i>			■	

Table 4.2 Anatomical characters of the laminae compared to different leaf forms occurring in section *Hoarea*. (Continue)

Leaf form / species	1	2	3	4
12. Pinnately compound, erect, irregularly bi- or tripinnatisect, aciculatum group				
<i>P. aciculatum</i>		■		
<i>P. confertum</i>		■		
<i>P. fasciculaceum</i>		■		
<i>P. connivens</i>		■		
1. Dorsiventral, spongy tissue loosely arranged				
2. Dorsiventral, spongy tissue compact				
3. Isobilateral, spongy tissue compact				
4. Stained layer				

Table 4.3 Anatomical characters of the laminae compared to different floral groups occurring in section *Hoarea*. (Species arranged according to floral groups)

Floral group / species	1	2	3	4
1. Fissifolium group				
<i>P. aestivale</i>	■			
<i>P. fissifolium</i>			■	
<i>P. petroselinifolium</i>			■	
<i>P. aristatum</i>		■	■	
2. Pinnatum group				
<i>P. chelidonium</i>				■
<i>P. nervifolium</i>	■			■
<i>P. pinnatum</i>		■	■	■
<i>P. reflexum</i>			■	
<i>P. violiflorum</i>	■			
3. Attenuatum group				
<i>P. attenuatum</i>				■
<i>P. angustipetalum</i>	■			■
<i>P. leptum</i>			■	■
<i>P. viciifolium</i>		■		■
<i>P. longifolium</i>			■	■
<i>P. fergusoniae</i>		■		■
<i>P. undulatum</i>			■	■
<i>P. longiflorum</i>			■	■
4. Proliferum group				
<i>P. proliferum</i>				■
<i>P. pilosellifolium</i>			■	■
<i>P. caledonicum</i>				
5. Heterophyllum group				
<i>P. heterophyllum</i>		■		
<i>P. tenellum</i>		■		
<i>P. trifoliolatum</i>			■	■
1. Dorsiventral, spongy tissue loosely arranged				
2. Dorsiventral, spongy tissue compact				
3. Isobilateral, spongy tissue compact				
4. Stained layer				

Table 4.3 Anatomical characters of the laminae compared to different floral groups occurring in section *Hoarea*. (Continue)

Floral group / species	1	2	3	4
6. Aciculatum group				
<i>P. aciculatum</i>		■		
<i>P. confertum</i>		■		
<i>P. fasciculaceum</i>		■		
<i>P. connivens</i>		■		
7. Luteum group				
<i>P. luteum</i>	■			
<i>P. fumarifolium</i>	■			■
8. Incrassatum group				
<i>P. incrassatum</i>			■	■
<i>P. grenvilleae</i>		■		■
<i>P. moniliforme</i>	■			
<i>P. vinaceum</i>	■			
<i>P. radicum</i>		■		
<i>P. appendiculatum</i>		■		
<i>P. campestre</i>				
<i>P. nephrophyllum</i>	■			
<i>P. carneum</i>			■	■
<i>P. radiatum</i>		■		
<i>P. nummulifolium</i>		■		
9. Luteolum group				
<i>P. luteolum</i>		■		■
<i>P. gracillimum</i>			■	
10. Rapaceum group				
<i>P. rapaceum</i>			■	
11. Auritum group				
<i>P. auritum</i> var. <i>auritum</i>			■	
<i>P. auritum</i> var. <i>carneum</i>			■	
<i>P. bubonifolium</i>			■	
<i>P. parvipetalum</i>			■	■
<i>P. leipoldtii</i>		■	■	
<i>P. ellaphieae</i>		■		
<i>P. asarifolium</i>		■		
<i>P. dipetalum</i>			■	■
<i>P. ternifolium</i>	■			■
12. Triphyllum group				
<i>P. triphyllum</i>	■			
13. Caroli-henrici group				
<i>P. githagineum</i>	■			
<i>P. caroli-henrici</i>		■		
<i>P. rubiginosum</i>		■		

Table 4.3 Anatomical characters of the laminae occurring with different floral groups occurring in section *Hoarea*. (Continue)

Floral group / species	1	2	3	4
14. Punctatum group				
<i>P. oblongatum</i>	■			
<i>P. curviandrum</i>	■			
<i>P. triandrum</i>	■			
<i>P. punctatum</i>	■			

1. Dorsiventral, spongy tissue loosely arranged
2. Dorsiventral, spongy tissue compact
3. Isobilateral, spongy tissue compact
4. Stained layer

Discussion

Comparing vegetative morphological characters to floral morphology, it confirms Dickison's (1975) statement that evolutionary modifications of vegetative characteristics are not necessarily closely synchronized with floral evolution (Table 3.6). Only the *Aciculatum* and the *Punctatum* floral groups are delimited by both the floral structure and the leaf form. When anatomical characters of the laminae are compared to leaf form (Table 4.2) or to floral structure (Table 4.3), these two groups again are delimited as taxonomic units. Relationships between smaller groups with similar floral structures and similar leaf forms are also confirmed by this comparison (Tables 4.4a).

Table 4.4a *Hoarea* species with similar floral structures, leaf form and lamina anatomy.

1.	<i>Aciculatum</i> group
2.	<i>Punctatum</i> group
3.	<i>P. moniliforme</i> and <i>P. vinaceum</i>
4.	<i>P. radiatum</i> and <i>P. nummulifolium</i>
5.	<i>P. heterophyllum</i> and <i>P. tenellum</i>
6.	<i>P. leptum</i> and <i>P. undulatum</i>
7.	<i>P. bubonifolium</i> and <i>P. parvipetalum</i>

This list of species with similar features is extended when the anatomy of the lamina is compared to floral structure only (Table 4.4b).

Table 4.4b *Hoarea* species with similar floral structures and lamina anatomy.

8.	<i>P. luteum</i> and <i>P. fumariifolium</i>
9.	<i>P. radicum</i> and <i>P. appendiculatum</i>
10.	<i>P. caroli-henrici</i> and <i>P. rubiginosum</i>

This comparison also reveals the diagnostic value of the anatomy of the lamina. Dorsiventral or isobilateral leaf architecture could be used to distinguish between species with similar leaf outlines (Table 4.5).

Table 4.5 Anatomy of the lamina of *Hoarea* species with similar leaf outlines.

Dorsiventral	Isobilateral	Floral structure
1. <i>P. luteolum</i>	<i>P. gracillimum</i>	similar
2. <i>P. reflexum</i>	<i>P. fergusoniae</i>	different
3. <i>P. longiflorum</i>	<i>P. radicum</i>	different
4. <i>P. longiflorum</i>	<i>P. ellaphieae</i>	different

At the same time the anatomy of the lamina could also be of diagnostic value if floral structures are compared (Table 4.6).

Table 4.6 Anatomy of the lamina of *Hoarea* species with similar floral structures.

Dorsiventral	Isobilateral	Leaf outline
1. <i>P. grenvillea</i>	<i>P. incrassatum</i>	different
2. <i>P. luteolum</i>	<i>P. gracillimum</i>	similar
3. <i>P. radiatum</i>	<i>P. carneum</i>	different
4. <i>P. nummulifolium</i>	<i>P. carneum</i>	different
5. <i>P. aestivale</i>	<i>P. fissifolium</i>	different
6. <i>P. aestivale</i>	<i>P. petroselinifolium</i>	different

The anatomy of the petiole does not contribute much to the delimitation of species or give any indication of trends of evolution in section *Hoarea*. The only useful character of the petiole anatomy is the absence of a medullary bundle in the petiole of *P. tenellum*. In *P. longifolium* a medullary bundle was lacking in some specimens, but not in all of them.

The presence or absence of sclerenchymatous tissue should rather be interpreted ecologically than giving it a taxonomic interpretation.

Anatomical characters of the lamina in section *Hoarea* are useful in the delimitation of some of the species. In other species similarities in the anatomy confirm relationships between species and do lend support to ideas formulated on macromorphology and pollen structure. Since similar anatomical structures have arisen many times in widely divergent taxa, similarities in structural specialization do not necessarily imply close relationship (Dickison 1975). For that reason I regard the support from the anatomy to the delimitation of smaller groups (Table 4.3) of more importance than the lack of it in the larger floral type groups.

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Table 4.7 Specimens of the different *Hoarea* species studied for leaf anatomy.

Taxon Specimen	Herbarium number	Taxon Specimen	Herbarium number
1. FISSIFOLIUM GROUP			
<i>P. aestivale</i>			
<i>Lavranos 20952</i>	STEU 3209	<i>Oliver s.n.</i>	STEU 442
<i>Van der Walt 1454</i>	STEU 3270	<i>Marais s.n.</i>	STEU 1740
<i>Marais 146</i>	STEU 3485	<i>Marais 209</i>	STEU 3642
<i>P. fissifolium</i>			
<i>Van der Walt s.n.</i>	STEU 1625	<i>Van der Walt 479</i>	STEU 554
<i>Fischer 133</i>	STEU 1928	<i>Marais 13</i>	STEU 2523
<i>Marais 232</i>	STEU 3667	<i>Marais 321</i>	STEU 3875
<i>Marais 249</i>	STEU 3684	<i>Marais 165</i>	STEU 3518
<i>P. petroselinifolium</i>			
<i>Fischer 356</i>	STEU 2688	<i>P. longifolium</i>	
<i>P. aristatum</i>			
<i>Fischer 27a</i>	STEU 1571	<i>Van der Walt s.n.</i>	STEU 1252
<i>Fischer 28</i>	STEU 1572	<i>Van der Walt 1060</i>	STEU 2440
<i>Van der Walt 1442</i>	STEU 3256	<i>Marais 57</i>	STEU 2920
<i>P. fergusoniae</i>			
2. PINNATUM GROUP			
<i>P. nervifolium</i>			
<i>Van der Walt s.n.</i>	STEU 1624	<i>Fischer 231</i>	STEU 2564
<i>Lavranos 18999</i>	STEU 2822	<i>Bayer 2513</i>	STEU 3153
<i>Marais 145</i>	STEU 3484	<i>Meve 261186/396</i>	STEU 3750
<i>Marais 274</i>	STEU 3711	<i>P. undulatum</i>	
<i>Marais 276</i>	STEU 3713	<i>Van der Walt s.n.</i>	STEU 1069
<i>Marais 334</i>	STEU 3897	<i>Lavranos 17470</i>	STEU 2310
<i>P. pinnatum</i> (* Large-flowered species)			
<i>Fischer 271</i>	STEU 2604*	<i>Van der Walt 1111</i>	STEU 2698
<i>Marais 169</i>	STEU 3544*	<i>Lavranos 18803</i>	STEU 2820
<i>Van der Walt 510</i>	STEU 584	<i>Muller 4141a</i>	STEU 3462
<i>Drijfhout 662</i>	STEU 856	<i>Marais 331</i>	STEU 3894
<i>Hugo s.n.</i>	STEU 1748	<i>P. longiflorum</i>	
<i>Lavranos 20905</i>	STEU 3206a	<i>Marais 35</i>	STEU 2665
<i>Muller s.n.</i>	STEU 3436	<i>Walters 3</i>	STEU 2987
<i>Marais 289</i>	STEU 3739	<i>Van der Walt 1412</i>	STEU 3181
<i>Van der Walt 1558</i>	STEU 3861	<i>Van der Walt 1421</i>	STEU 3190
<i>P. reflexum</i>			
<i>Van Wyk 161</i>	STEU 2129	<i>Marais 182</i>	STEU 3555
<i>Marais 278</i>	STEU 3715	<i>Marais 267</i>	STEU 3704
<i>P. violiflorum</i>			
<i>Fischer 216</i>	STEU 2548	<i>Marais 268</i>	STEU 3705
<i>Marais 308</i>			
<i>Le Maitre s.n.</i>			
<i>STEU 3839</i>			
4. PROLIFERUM GROUP			
<i>P. pilosellifolium</i>			
3. ATTENUATUM GROUP			
<i>P. angustipetalum</i>			
<i>Drijfhout 1371</i>	STEU 674	<i>Schonken 201</i>	STEU 2174
<i>P. heterophyllum</i>			
<i>Van der Walt 1041</i>			
<i>Marais 33</i>			
<i>STEU 2408</i>			
<i>STEU 2663</i>			

Table 4.7 (Continue)

Taxon Specimen	Herbarium number	Taxon Specimen	Herbarium number
<i>P. tenellum</i>		8. INCRASSATUM GROUP	
Van der Walt 1027	STEU 2395	<i>P. incrassatum</i>	
Van Zyl s.n.	STEU 3253	Boucher 63	STEU 989
Marais 136	STEU 3453		
Van Zyl s.n.	STEU 3884	Van der Walt 789	STEU 1525
<i>P. trifoliolatum</i>		Fischer 1	STEU 1545
Cillié s.n.	STEU 589	Marais 74	STEU 3320
Marais 40	STEU 2673	<i>P. grenvilleae</i>	
Marais 45	STEU 2680	Van der Walt 1406	STEU 3170
Marais 178	STEU 3551	Marais 131	STEU 3428
Marais 300	STEU 3779	Williamson 3951	STEU 3911
Marais 345	STEU 3941	Williamson 3950	STEU 3913
6. ACICULATUM GROUP		<i>P. moniliforme</i>	
<i>P. aciculatum</i>		Boucher 77	STEU 996
Ward s.n.	STEU 1098	Lavranos 17478	STEU 2324
Van der Walt 1024	STEU 2282	Marais 73	STEU 3318
Van der Walt 1039	STEU 2405	Marais 217	STEU 3652
Marais 265	STEU 3702	Marais 355	STEU 3996
<i>P. confertum</i>		<i>P. vinaceum</i>	
Van der Walt 956	STEU 2069	Lavranos 20785	STEU 3220
Van Jaarsveld 4283	STEU 2375	Marais 77	STEU 3339
Marais 72	STEU 3317	Williamson 3527	STEU 3626
<i>P. fasciculaceum</i>		Visser s.n.	STEU 3859
Van der Walt 1046	STEU 2420	Williamson 4010	STEU 3915
Marais 184	STEU 3557	<i>P. radicum</i>	
Marais 199	STEU 3632	Van der Walt 1417	STEU 3186
Marais 266	STEU 3703	<i>P. appendiculatum</i>	
<i>P. connivens</i>		Van der Walt 1429	STEU 3233
Lavranos 19001	STEU 2817	<i>P. nephrophyllum</i>	
Lavranos 19000	STEU 2824	Snijman 593	STEU 3229
7. LUTEUM GROUP		<i>P. carneum</i>	
<i>P. luteum</i>		Fischer 363	STEU 2826
Marais 120	STEU 3417	Marais 147	STEU 3486
Marais 121	STEU 3418	Marais 153	STEU 3491
Perry 3243	STEU 3449	Marais 154	STEU 3492
Marais 270	STEU 3707	<i>P. radiatum</i>	
Marais 271	STEU 3708	Van der Walt 970	STEU 2114
<i>P. fumariifolium</i>		Van der Walt 1063	STEU 2443
Marais 240	STEU 3675	Van der Walt 1494	STEU 3476
Marais 391	STEU 4100	Albers s.n.	STEU 3728

Table 4.7 (Continue)

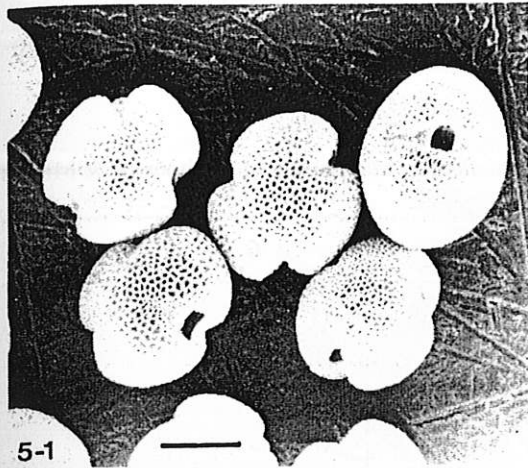
Taxon Specimen	Herbarium number	Taxon Specimen	Herbarium number
<i>P. nummulifolium</i> Watson 71	STEU 3954	Van Wyk 752	STEU 3063
9. LUTEOLUM GROUP		<i>P. dipetalum</i> Marais 173	STEU 3548
<i>P. luteolum</i> Lavranos 20266	STEU 3105	<i>P. ternifolium</i> Drijfhout 1627	STEU 855
<i>P. gracillimum</i> Marais 161	STEU 3499	Marais s.n.	STEU 1741
Marais 162	STEU 3500	Marais 319	STEU 3873
		Marais 320	STEU 3874
10. RAPACEUM GROUP		12. TRIPHYLLUM GROUP	
<i>P. rapaceum</i> Marais 122	STEU 3419	<i>P. triphyllum</i> Von Willert s.n.	STEU 4096
Marais 200	STEU 3633	13. CAROLI-HENRICI GROUP	
Van Zyl s.n.	STEU 3886	<i>P. githagineum</i> Lavranos 20785a	STEU 3220a
11. AURITUM GROUP		Marais 143	STEU 3482
<i>P. auritum</i> v <i>auritum</i> Marais 96	STEU 3393	Marais 243	STEU 3678
Marais 314	STEU 3868	<i>P. caroli-henrici</i> Drijfhout 2708	STEU 2889
<i>P. auritum</i> v <i>carneum</i> Lavranos 20926	STEU 3216	Marais 281	STEU 3718
Marais 156	STEU 3494	<i>P. rubiginosum</i> Van Jaarsveld 4100	STEU 2371
Marais 160	STEU 3498	Drijfhout 2811	STEU 2888
<i>P. bubonifolium</i> Van Jaarsveld 4230	STEU 2370	14. PUNCTATUM GROUP	
Drijfhout 2971	STEU 2886	<i>P. oblongatum</i> Van der Walt s.n.	STEU 819
Drijfhout 2970	STEU 2895	Van Jaarsveld 5368	STEU 2887
<i>P. parvipetalum</i> Bruyns 1519	STEU 1455	<i>P. curviandrum</i> Lavranos 20941	STEU 3214
Stirton 9242	STEU 3066	<i>P. triandrum</i> Van der Walt s.n.	STEU 1464
<i>P. leipoldtii</i> Walters 2	STEU 2986	Van der Walt s.n.	STEU 1477
Muller 4036	STEU 3465	Friedrich 452	STEU 2184
Marais 207	STEU 3640	Van der Walt 1276	STEU 2947
Marais 220	STEU 3655	Van Niekerk s.n.	STEU 3627
Van Zyl s.n.	STEU 3973	<i>P. punctatum</i> Fischer 34	STEU 1578
<i>P. ellaphieae</i> Marais 305	STEU 3817	Van der Walt 944	STEU 2057
Marais 306	STEU 3818	Lavranos 18876	STEU 2821
Marais 383	STEU 4085	Marais 67	STEU 3302
<i>P. asarifolium</i> Van der Walt 1062	STEU 2442	Meve 273	STEU 3744
Fischer 343	STEU 2475		

CHAPTER 5

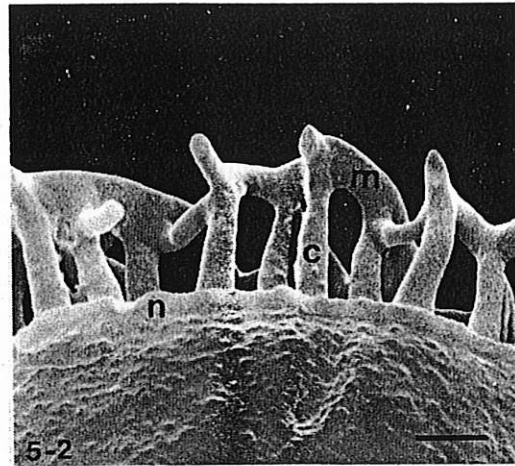
PALYNOLOGY

Data from pollen grains are known to be useful at all levels of the taxonomic hierarchy and data obtained with the help of the scanning electron microscope are often most valuable at the lower levels of the taxonomic hierarchy (Stuessy 1990). It is also known that in some genera no significant differences are found among the different species, whereas in others remarkable variations of great and obvious taxonomic value occur. Several studies investigated the taxonomic value of the pollen morphology of the Geraniaceae. According to Bortenschlager (1967) the pollen morphology of the different genera of the Geraniaceae is heterogeneous. *Pelargonium* was shown to have some affinities with the related genera *Erodium* L'Hérit., *Monsonia* L. and *Sarcocaulon*. All five genera of the Geraniaceae have representatives with a reticulate exine, but in *Erodium* and *Geranium* a reticulate to striate pattern occurs. In their study of the pollen of *Sarcocaulon*, Verhoeven & Venter (1988) failed to produce any diagnostic characters of the exine within the genus, but pollen size might be useful in some cases to distinguish between species. Pollen data support the close relationship between *Sarcocaulon* and *Monsonia* L. (Verhoeven & Venter 1986). Except for *M. speciosa* L. and *M. deserticola* Dinter ex Knuth, pollen morphology of *Monsonia* cannot be used to distinguish between different species, but is useful in grouping species into four different pollen types, and according to Verhoeven & Venter (1986) pollen morphology supports the present taxonomic division of the genus. In respect to pollen size and density of suprategal processes in the European representatives of *Geranium* L., Stafford and Blackmore (1991) identified four different groups. They observed a certain degree of overlap between the four groups. Although the southern African *Geranium* species cannot be grouped in a similar way, pollen size plays an important role in grouping these species (Verhoeven & Venter 1992). In *Erodium* different pollen types are identified (El-Oqlah 1983, Verhoeven & Venter 1987) but because of the variation in the sculpture within the same species, the pollen morphology is of little taxonomic value in this genus.

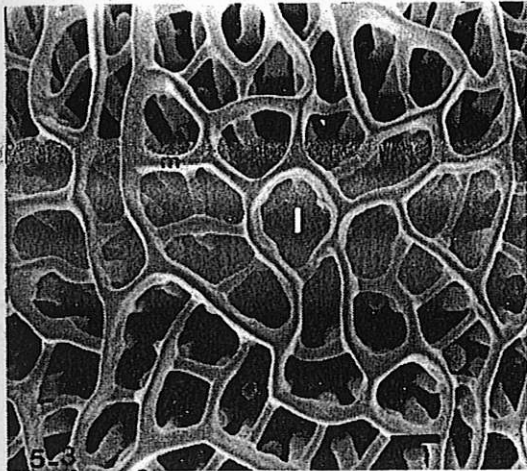
In *Pelargonium* pollen morphology is useful in the delimitation of the different sections. In the case of section *Polyactium* pollen morphology confirms the delimitation of the subsections (Marais 1981, Verhoeven & Marais 1990). In most cases pollen morphology cannot be used to distinguish between closely related species in *Pelargonium*, but there are cases in which the presence or absence of intraluminary baculae (Bortenschlager 1967, Dreyer 1990a) and the size of the pollen grains exhibit differences at species level. In *Pelargonium* several examples are known where pollen



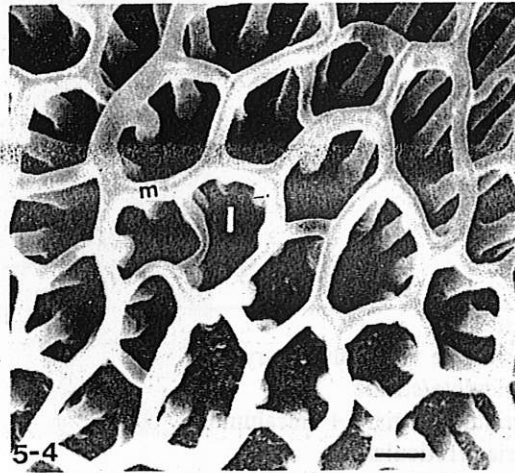
5-1



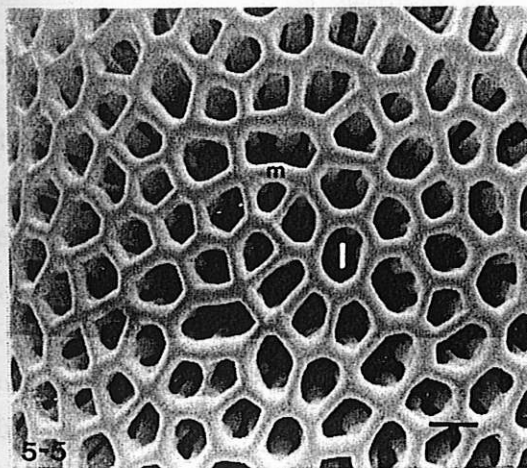
5-2



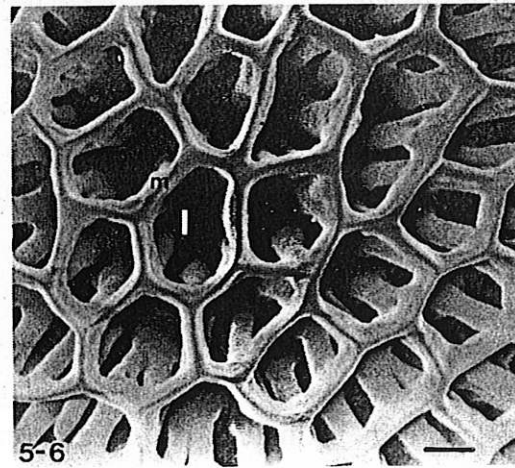
5-3



5-4



5-5



5-6

Figure 5.1 Pollen grains of *P. undulatum* (Van der Walt s.n., STEU 1069). Scale bar: 30 μm .

Figure 5.2 Pollen wall of *P. carneum* (Van der Walt s.n., STEU 1654). Scale bar: 2 μm .

Figure 5.3 Mesocolpium of the pollen of *P. luteum* (Marais 270). Scale bar: 2 μm .

Figure 5.4 Mesocolpium of the pollen of *P. fissifolium* (Drijfhout 2657). Scale bar: 2 μm .

Figure 5.5 Mesocolpium of the pollen of *P. proliferum* (Van der Walt 931). Scale bar: 2 μm .

Figure 5.6 Mesocolpium of the pollen of *P. longifolium* (Van der Walt 1060), Scale bar: 2 μm .

c = columella, l = lumen, m = muri, n = nexine.

morphology confirms the misplacement of species by Knuth (1912) in sections with non-related species (Verhoeven & Marais 1990).

Table 5.1 Type of tectum structures in the different sections of *Pelargonium*. (From Verhoeven & Marais 1990)

	1	2	3	4	5	6	7
<i>Eumorpha</i>				+	+		
<i>Pelargonium</i>				+ -	+		
<i>Glaucophyllum</i>			+		+		
<i>Dibrachya</i>					+		
<i>Ciconium</i>					+		
<i>Isopetalum</i>					+		
<i>Campylia</i>					+		
<i>Peristera</i>	+		+		+		
<i>Cortusina</i>	+	+	+		+		
<i>Reniformia</i>			+		+		
<i>Polyactium</i>	+				+		+
<i>Ligularia s.l.</i>	+	+	+	+	+		
<i>Myrrhidium</i>					+		
<i>Jenkinsonia</i>					+		
<i>Otidia</i>					+		
<i>Hoarea</i>	+		+	+	+	+	

1 = reticulate
 2 = reticulate + intraluminary baculae
 3 = reticulate/striate
 4 = reticulate/striate + intraluminary baculae
 5 = striate/reticulate
 6 = striate
 7 = double structure: Pole: striate
 Mesocolpium: striate/reticulate

! = prominent
 - = seldom present

Taxonomic characters provided by pollen grains include aggregation, shape and size of the grains, number, shape and position of apertures and the ornamentation of the wall, that is primarily the exine (Jones & Luchsinger 1987, Stuessy 1990), thus resulted in the description of *Pelargonium* pollen grains as spherical, radiosymmetric, isopolar, tricolporate monades (Figure 5.1, Bortenschlager 1967, Verhoeven & Marais 1990). According to Walker & Doyle's (1975) criteria, the pollen grains are large (50 to 100 μm in diameter). The exine consists of a nexine and sexine. The latter is semitectate and consists of columellae and a tectum (Figure 5.2). Bortenschlager (1967) distinguished different patterns in the arrangement of the muri in the tectum and described these as reticulate, reticulate-striate, striate-reticulate and striate. In the majority of species of *Pelargonium* the structure of the tectum is striate-reticulate because some muri are on a higher level and appear more or less parallel to each other and more prominent than others (Figure 5.3). This pattern is represented in all the sections in *Pelargonium* (Table 5.1, Verhoeven & Marais 1990). Sometimes the minor muri are more or less on the same level as the parallel ones and the tectum appears to be reticulate-striate (Figure 5.4).

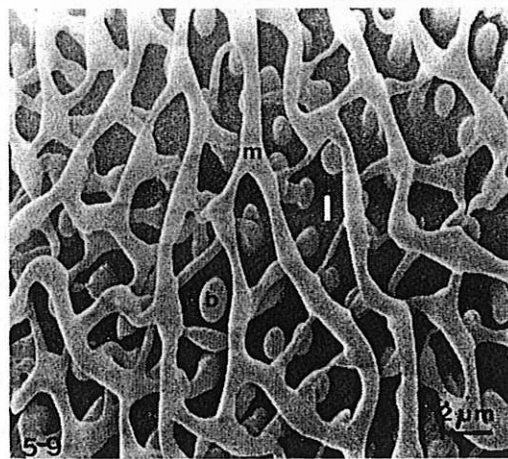
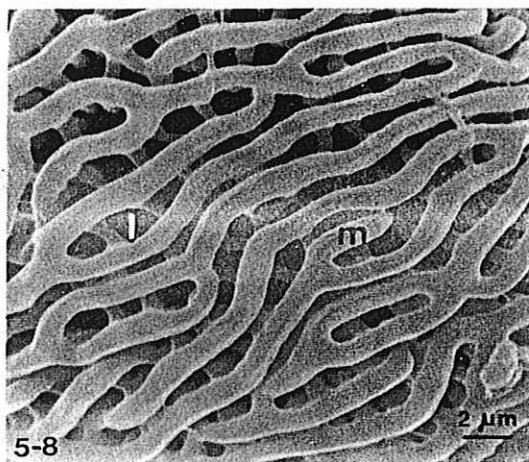
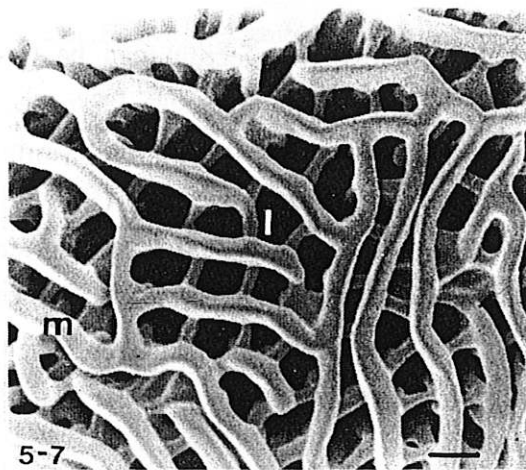


Figure 5.7 Mesocolpium of the pollen of *P. radicum* (Niven s.n. (S)). Scale bar: 2 μm .

Figure 5.8 Mesocolpium of the pollen of *P. punctatum* (Van der Walt 944). Scale bar: 2 μm .

Figure 5.9 Mesocolpium of the pollen of *P. nummulifolium* (Watson 71). Scale bar: 2 μm .

b = intraluminary bacula l = lumen, m = muri.

When all the muri are on the same level the tectum can be described as reticulate. (Figures 5.5 & 5.6) In section *Ligularia* (species *P. otaviense* Knuth and *P. grandicalcaratum* Knuth) a reticulate ornamentation with minute luminae occurs (Verhoeven & Marais 1990, Van der Walt, Albers & Gibby 1990), and could be described as tectate perforate (Walker & Doyle 1975). Another feature of the tectum is the presence of intraluminary baculae (Bortenschlager 1967). In section *Cortusina sensu stricto* these baculae are very prominent in some species, but are lacking in others (Dreyer 1990a). Intraluminary baculae are present in other sections also, but never as prominent as in section *Cortusina*.

Results

The pollen morphology of section *Hoarea* fits in well with the rest of the genus. The variation in the tectum includes all patterns present in the genus except that of *P. otaviense* and *P. grandicalcaratum*, and the double structure occurring in section *Polyactium* (Verhoeven & Marais 1990). In section *Hoarea* the reticulate pattern is represented by one with small luminae like in *P. proliferum* (Figure 5.5), and another one where the luminae are larger like in *P. longifolium*. (Figure 5.6). The tectum of some species in section *Hoarea* can be described as striate because the main, parallel muri are much thicker and more prominent than the lower connecting ones (Figure 5.7), and in some cases an extremely striate pattern of the tectum occurs that does not occur in the any other section of *Pelargonium* (Figure 5.8). In most cases the reticulate pattern on one side and the extreme form of striate pattern on the other side can easily be recognized, but the reticulate-striate and striate-reticulate ornamentations are difficult to distinguish and transitional forms occur throughout the whole spectrum. Because of these transitional forms and the difficulty with which border lines are established between the three main tectum patterns (reticulate, striate-reticulate and striate), these patterns were subdivided, each receiving a qualitative value of one to six (see key to Table 5.2). No measurements of lumina sizes were taken. The shape of the pollen grains and the details of the apertures are more or less the same in all *Pelargonium* species and do not get any attention here. Specimens studied as well as the equatorial diameters of the pollen grains are listed in Table 5.3.

Table 5.2 Pollen grains of section *Hoarea*: (a) structure of the tectum; (b) equatorial diameter.

Species	(a) Tectum structure							(a) Equatorial diameter (μm)				
	1	2	3	4	5	6	7	40	50	60	70	80 μm
Fissifolium group												
<i>P. aestivale</i>			*							—		
<i>P. fissifolium</i>			*						—	—		
<i>P. petroselinifolium</i>			*						—			
<i>P. aristatum</i>			*						—			
Pinnatum group												
<i>P. chelidonium</i>				*					—	—		
<i>P. nervifolium</i>				*					—	—		
<i>P. pinnatum</i>		*								—	—	
<i>P. reflexum</i>		*							—	—		
<i>P. violiflorum</i>		*							—	—		
Attenuatum group												
<i>P. attenuatum</i>				*					—	—		
<i>P. angustipetalum</i>				*					—			
<i>P. leptum</i>		*					+		—			
<i>P. viciifolium</i>		*					+		—	—		
<i>P. longifolium</i>		*							—	—		
<i>P. fergusoniae</i>		*							—	—		
<i>P. undulatum</i>		*							—	—		
<i>P. longiflorum</i>		*							—	—		
Proliferum group												
<i>P. proliferum</i>	*								—			
<i>P. pilosellifolium</i>	*								—	—		
<i>P. caledonicum</i>	*								—	—		
Heterophyllum group												
<i>P. heterophyllum</i>					*				—			
<i>P. tenellum</i>					*				—			
<i>P. trifoliolatum</i>					*					—		
Aciculatum group												
<i>P. aciculatum</i>					*					—	—	
<i>P. confertum</i>					*					—	—	
<i>P. fasciculaceum</i>					*					—	—	
<i>P. connivens</i>					*					—	—	
Luteum group												
<i>P. luteum</i>				*						—		
<i>P. fumariifolium</i>				*						—		

- 1 = reticulate, small luminae
- 2 = reticulate, large luminae
- 3 = reticulate-striate
- 4 = striate-reticulate

- 5 = striate
- 6 = extremely striate
- 7 = intraluminary baculae

Table 5.2 Continue

Species	(a) Tectum structure							(a) Equatorial diameter (μm)					
	1	2	3	4	5	6	7	40	50	60	70	80 μm	
Incrassatum group													
<i>P. incrassatum</i>					*						—		
<i>P. grenvilleae</i>					*						—		
<i>P. moniliforme</i>					*					—			
<i>P. vinaceum</i>					*					—			
<i>P. radicum</i>					*					—			
<i>P. appendiculatum</i>				*								—	
<i>P. campestre</i>				*							—		
<i>P. nephrophyllum</i>				*							—		
<i>P. carneum</i>				*								—	
<i>P. radiatum</i>				*								—	
<i>P. nummulifolium</i>				*			+				—		
Luteolum group													
<i>P. luteolum</i>				*						—			
<i>P. gracillimum</i>				*					—				
Rapaceum group													
<i>P. rapaceum</i>				*						—			
Auratum group													
<i>P. auratum</i> v <i>auratum</i>				*						—			
<i>P. auratum</i> v <i>carneum</i>				*						—			
<i>P. bubonifolium</i>				*						—			
<i>P. parvipetalum</i>				*						—			
<i>P. leipoldtii</i>				*						—			
<i>P. ellaphieae</i>				*						—			
<i>P. asarifolium</i>				*						—			
<i>P. dipetalum</i>				*			+			—			
<i>P. ternifolium</i>				*			+			—			
Triphyllum group													
<i>P. triphyllum</i>				*						—			
Caroli-henrici group													
<i>P. githagineum</i>				*			+				—		
<i>P. caroli-henrici</i>				*						—			
<i>P. rubiginosum</i>							*			—			
Punctatum group													
<i>P. oblongatum</i>				*								—	
<i>P. curviandrum</i>				*								—	
<i>P. triandrum</i>							*				—		
<i>P. punctatum</i>							*			—			

Discussion

Hemsley and Ferguson (1985) pointed out that in palynological contributions to taxonomy the emphasis so far, was on the comparative studies of structure and ornamentation among pollen. Only recently the attention has been shifted to the functional aspects of the structural details. According to them it seems reasonable to expect that pollen, subject to natural selection just as much as the whole plant, has evolved to meet the demands imposed upon them. Therefore I regard that the evolution in the floral structure of *Hoarea*, was accompanied by a co-evolution of the pollen grains. With this in mind section *Hoarea* was divided into different groups on the basis of floral morphology with the accent on the structure of the androecium, and the pollen morphology also playing a role in this planning (Table 5.2).

According to Stafford & Gibby (1992) pollen size may be significant in delimiting some sections within the genus. This does not apply for the section *Hoarea*, because the equatorial diameter for the different species studied varies from 43 to 95 μm (Tables 5.2 & 5.3). That is almost representative of the whole spectrum for the genus (Stafford & Gibby 1992). However, in some floral type groups in *Hoarea*, pollen size could be one of the contributing factors in delimiting the groups (Table 5.2), but this does not apply to all the groups. On the other hand, polyploid species can have larger pollen grains than closely related diploid ones (Dreyer *et al.* 1992), but polyploidy versus pollen grain size can only be verified when the chromosome numbers become available.

The average diameters of the pollen grains of species with short stamens (*Fissifolium*, *Pinnatum*, *Attenuatum* and *Proliferum* groups) vary between 48 and 66 μm , which delimit these species as a group with medium size pollen grains. Although there is a variation in the form and size of the petals of these species, the stamens are always shorter than the sepals and concealed within the floral sheath. There is a slight variation in the ornamentation of the tectum in this group and it varies from reticulate (with small luminae and with large luminae) to reticulate-striate. However, in *P. attenuatum* and *P. angustipetalum*, two very closely related species, the tectum could rather be described as striate-reticulate. Within this larger group the *Proliferum* group can be delimited as a taxonomic unit because of the small petals and the uniformity of the tectum ornamentation (Table 5.2).

Although there is a noticeable variation in the size of the pollen grains of the *Heterophyllum* group, the delimitation of this group on the basis of the androecium structure, is confirmed by the homogeneous pattern of the tectum. The *Aciculatum* group

as well as the *Auratum* group are delimited on the basis of floral structure, tectum ornamentation as well as pollen size (Table 5.2).

The *Incrassatum* group seems to be heterogeneous with regard to tectum ornamentation as well as pollen size. This group is delimited on the basis of long, straight, protruding stamens, with an obvious difference in the length of the posterior, the lateral and anterior stamens. It is also characterized by the differences in the form and size of the petals of the different species. The *Caroli-henrici* and the *Punctatum* groups seem both to be heterogeneous with respect to pollen size and pollen structure.

In several cases in section *Hoarea* the size of the pollen grains can be used to distinguish between species with similar floral structures and similar ornamentations of the tectum. The pollen grains of *P. trifoliolatum* (62--67 μm) are larger than those of the related *P. heterophyllum* (49--50 μm) and *P. tenellum* (51--56 μm). The same accounts for the two related species *P. luteolum* (53--62 μm) and *P. gracillimum* (43--58 μm) and for another two species: *P. luteum* (58--67 μm) and *P. fumariifolium* (49--55 μm). The pollen grains of *P. punctatum* (57--60 μm in diameter) and *P. triandrum* (70--85 μm in diameter), species with similar floral structures and in both cases an extremely striate ornamentation of the tectum, reveal a remarkable difference in size (Table 5.2).

The flowers of *P. appendiculatum* and *P. radicum* are seemingly very similar. However, the ornamentation of the tectum shows a slight difference between the two species and the pollen size a remarkable one. Pollen grains of *P. appendiculatum* vary between 77 to 85 μm in diameter and those of *P. radicum* between 60 to 68 μm .

In *P. pinnatum* pollen size of small-flowered individuals varies between 57 and 65 μm and those of large-flowered individuals between 69 and 71 μm (Marais 1993). The occurrence of polyploidy in large-flowered individuals in this case should be investigated.

Although the presence of intraluminary baculae is never so prominent in section *Hoarea* as in section *Cortusina* (Dreyer 1990a), and although I do not regard the occasional presence of intraluminary baculae in most species as of any significance, there are cases where these baculae are noticeable, like in *P. nummulifolium* (Figure 5.9), where their presence delimits this species from the closely related *P. radiatum*. Intraluminary baculae are lacking in the latter.

The most important contribution of the pollen morphology to the taxonomy of section *Hoarea* is the delimitation of smaller groups within the section and the structure of the

teetum supports to a large extent the proposed grouping of species in respect to the structure of the androecium. Although this is mainly based on the ornamentation of the teetum, the size of the pollen grains also plays a role in this demarcation. However, this is not the case for all the floral groups in section *Hoarea*. In some cases pollen size plays a significant role in the delimitation of species and a character to be used to distinguish between species. Pollen morphology suggests the heterogeneity of the composition of the *Caroli-henrici* as well as the *Punctatum* groups (Table 5.2).

Phylogeny

Although it is generally accepted that a reticulate ornamentation represents the primitive type of teetum, a view also held by Stafford & Gibby (1992), I regard the striate-reticulate teetum to be the primitive type in the case of *Pelargonium*. This I base on a statement made by Walker & Doyle (1975) on the evolution of pollen wall architecture, that sculpturing itself undoubtedly represents a more or less reversible character which must be interpreted in terms of individual correlations observed within any given taxa. The striate-reticulate pattern is present in all the sections of *Pelargonium* (Table 5.1). It is also the only type of teetum present in section *Pelargonium*, a section with many other primitive characters also (Van der Walt 1985, Van der Walt & Roux 1991). Reticulate and striate patterns of the teetum can be regarded as derived conditions. The extremely striate pattern, occurring in *P. punctatum*, *P. triandrum* and *P. rubiginosum*, is associated with the reduction in the number of fertile stamens and in some cases also with the reduction in the number of filaments and carpels. The reduction in the number of floral parts is regarded as a derived character (Radford *et al.* 1974). Therefore the extremely striate pattern of the teetum of *P. punctatum*, *P. triandrum* and *P. rubiginosum* can be regarded as the most advanced type of pollen structure in *Pelargonium*.

Table 5.3 Specimens of *Hoarea* species studied for pollen grain morphology and the equatorial measurements.

Taxon Specimen	Herbarium number	Pollen measurements		
		Min	Max	x (μm)
1. FISSIFOLIUM GROUP				
<i>P. aestivale</i>				
<i>Lavranos 20952</i>	STEU 3209	54	66	59
<i>Van der Walt 1454</i>	STEU 3270	49	62	57
<i>Marais 146</i>	STEU 3485	52	69	60
<i>P. fissifolium</i>				
<i>Fischer 133</i>	STEU 1928	52	66	59
<i>Van der Walt 1057</i>	STEU 2438	49	57	53
<i>Drijfhout 2657</i>	STEU 2757	47	59	54
<i>Marais 249</i>	STEU 3684	49	59	52
<i>Marais 348</i>	STEU 3989	49	74	61
<i>Marais 354</i>	STEU 3995	54	66	61
<i>P. petroselinifolium</i>				
<i>Lavranos 17471</i>	STEU 2315	47	62	56
<i>Fischer 356</i>	STEU 2688	47	57	53
<i>Marais 65</i>	STEU 3340	49	64	55
<i>P. aristatum</i>				
<i>Fischer 27a</i>	STEU 1571	46	55	51
<i>Fischer 28</i>	STEU 1572	48	58	52
<i>Schonken 215</i>	STEU 2308	46	60	53
<i>Van der Walt 1442</i>	STEU 3256	46	58	51
2. PINNATUM GROUP				
<i>P. chelidonium</i>				
<i>Marais 261</i>	STEU 3696	48	62	56
<i>P. nervifolium</i>				
<i>Van der Walt s.n.</i>	STEU 1624	55	60	59
<i>Lavranos 18999</i>	STEU 2822	55	65	60
<i>Marais 141</i>	STEU 3480	55	62	59
<i>Marais 145</i>	STEU 3484	50	58	54
<i>Marais 253</i>	STEU 3688	55	65	60
<i>P. pinnatum</i> (* Large-flowered specimens)*				
<i>Vorster 2905</i>	STEU 2478*	64	76	71
<i>Vorster 2917</i>	STEU 2491*	56	74	69
<i>Marais 169</i>	STEU 3544*	61	76	70
<i>Van der Walt 510</i>	STEU 584	56	69	61
<i>Drijfhout 662</i>	STEU 856	56	69	62
<i>Hugo s.n.</i>	STEU 1748	54	74	65
<i>Marais 32</i>	STEU 2662	49	61	57
<i>Lavranos 20905</i>	STEU 3206a	61	69	64
<i>P. reflexum</i>				
<i>Van Wyk 161</i>	STEU 2129	50	65	57
<i>P. violiflorum</i>				
<i>Fischer 216</i>	STEU 2548	50	60	55

Table 5.3 (Continue)

Taxon Specimen	Herbarium number	Pollen measurements		
		Min	Max	x (μm)
3. ATTENUATUM GROUP				
<i>P. attenuatum</i>				
<i>Smit s.n.</i>	STEU 3221	43	58	51
<i>P. angustipetalum</i>				
<i>Drijfhout 1371</i>	STEU 674	43	55	51
<i>Roux 265</i>	STEU 3252	43	50	48
<i>Meve 236</i>	STEU 3745	46	53	49
<i>P. leptum</i>				
<i>Oliver s.n.</i>	STEU 442	48	58	53
<i>Marais s.n.</i>	STEU 1740	53	58	55
<i>P. viciifolium</i>				
<i>Van der Walt 479</i>	STEU 554	49	61	59
<i>Marais 13</i>	STEU 2523	54	66	61
<i>Marais 134</i>	STEU 3451	44	59	52
<i>Marais 321</i>	STEU 3875	44	61	51
<i>P. longifolium</i>				
<i>Van der Walt s.n.</i>	STEU 1252	46	55	51
<i>Van der Walt 1060</i>	STEU 2440	50	65	57
<i>Marais 57</i>	STEU 2920	50	58	54
<i>P. fergusoniae</i>				
<i>Fischer 231</i>	STEU 2564	48	60	55
<i>Fischer 304</i>	STEU 2636	48	55	52
<i>Bayer 2513</i>	STEU 3153	46	55	52
<i>P. undulatum</i>				
<i>Van der Walt s.n.</i>	STEU 1069	55	62	58
<i>Lavranos 18803</i>	STEU 2820	53	62	58
<i>Van der Walt 1593</i>	STEU 4062	50	65	57
<i>P. longiflorum</i>				
<i>Schonken 37</i>	STEU 1533	47	71	50
<i>Marais 35</i>	STEU 2665	47	71	51
<i>Van der Walt 1421</i>	STEU 3190	47	71	50
<i>Marais 182</i>	STEU 3555	59	71	66
<i>Marais 267</i>	STEU 3704	43	50	47
<i>Marais 308</i>	STEU 3820	43	55	49
<i>Le Maitre s.n.</i>	STEU 3839	50	62	57
4. PROLIFERUM GROUP				
<i>P. proliferum</i>				
<i>Van der Walt 931</i>	STEU 1940	46	55	50
<i>Van der Walt 1083</i>	STEU 2469	41	53	47
<i>Fischer 302</i>	STEU 2634	46	55	50
<i>Van der Walt 1428</i>	STEU 3222	43	55	48
<i>Marais 85</i>	STEU 3360	48	60	50
<i>Cillié s.n.</i>	STEU 3368	41	53	47

Table 5.3 (Continue)

Taxon Specimen	Herbarium number	Pollen measurements		
		Min	Max	x (μm)
<i>P. pilosellifolium</i>				
<i>Schonken 201</i>	STEU 2174	48	53	50
<i>Fischer 293</i>	STEU 2626	46	53	48
<i>Fischer 365</i>	STEU 2828	41	53	48
<i>Lavranos 20911</i>	STEU 3213	46	53	50
<i>P. caledonicum</i>				
<i>Van der Walt s.n.</i>	STEU 1596a	46	60	54
<i>Van der Walt 1093</i>	STEU 2506	46	60	54
<i>Fischer 268</i>	STEU 2601	48	60	55
5. HETEROPHYLLUM GROUP				
<i>P. heterophyllum</i>				
<i>Van der Walt 1041</i>	STEU 2408	48	53	50
<i>Marais 33</i>	STEU 2663	43	58	49
<i>P. tenellum</i>				
<i>Van der Walt 1027</i>	STEU 2395	50	60	56
<i>Marais 15</i>	STEU 2531	43	60	54
<i>Van Zyl s.n.</i>	STEU 3253	50	60	55
<i>Marais 136</i>	STEU 3453	41	55	51
<i>P. trifoliolatum</i>				
<i>Cillié s.n.</i>	STEU 589	56	74	62
<i>Marais 40</i>	STEU 2673	56	76	66
<i>Marais 45</i>	STEU 2680	61	76	67
6. ACICULATUM GROUP				
<i>P. aciculatum</i>				
<i>Ward s.n.</i>	STEU 1098	57	69	61
<i>Van der Walt 1024</i>	STEU 2282	59	79	70
<i>Van der Walt 1039</i>	STEU 2405	56	71	65
<i>Marais 265</i>	STEU 3702	68	76	72
<i>P. confertum</i>				
<i>Van der Walt 956</i>	STEU 2069	66	81	74
<i>Van Jaarsveld 4283</i>	STEU 2375	64	79	73
<i>Marais 72</i>	STEU 3317	67	86	79
<i>P. fasciculaceum</i>				
<i>Van der Walt 1046</i>	STEU 2420	62	86	74
<i>Marais 184</i>	STEU 3557	66	74	70
<i>Marais 199</i>	STEU 3632	74	86	82
<i>Marais 266</i>	STEU 3703	66	81	74
<i>Von Willert s.n.</i>	STEU 3756	64	79	72
<i>Marais 325</i>	STEU 3880	66	86	75
<i>P. connivens</i>				
<i>Lavranos 19001</i>	STEU 2817	59	76	70
<i>Lavranos 19000</i>	STEU 2824	71	86	79

Table 5.3 (Continue)

Taxon Specimen	Herbarium number	Pollen measurements		
		Min	Max	x (μm)
7. LUTEUM GROUP				
<i>P. luteum</i>				
<i>Fischer 33</i>	STEU 1577a	53	62	58
<i>Perry 3243</i>	STEU 3449	60	74	67
<i>Marais 270</i>	STEU 3707	53	72	62
<i>Marais 271</i>	STEU 3708	58	67	63
<i>P. fumariifolium</i>				
<i>Marais 240</i>	STEU 3675	50	60	55
<i>Marais 391</i>	STEU 4100	46	55	48
8. INCRASSATUM GROUP				
<i>P. incrassatum</i>				
<i>Van der Walt 789</i>	STEU 1525	65	72	68
<i>Fischer 1</i>	STEU 1545	62	70	67
<i>Drijfhout 2942</i>	STEU 2890	60	67	64
<i>P. grenvilleae</i>				
<i>Van der Walt 1406</i>	STEU 3170	62	70	66
<i>Marais 131</i>	STEU 3428	60	67	64
<i>Williamson 3951</i>	STEU 3911	53	72	65
<i>Williamson 3950</i>	STEU 3913	60	67	64
<i>P. moniliforme</i>				
<i>Boucher 77</i>	STEU 996	50	62	59
<i>Marais 68</i>	STEU 3303	58	62	59
<i>Marais 75</i>	STEU 3321	53	60	57
<i>Marais 355</i>	STEU 3996	58	65	61
<i>P. vinaceum</i>				
<i>Lavranos 20785</i>	STEU 3220	55	72	62
<i>Marais 77</i>	STEU 3339	55	65	59
<i>Van Jaarsveld 9695</i>	STEU 3858	53	72	65
<i>Williamson 4010</i>	STEU 3915	53	70	61
<i>P. radicum</i>				
<i>Bachman 1533</i>	Z	53	65	60
<i>Niven s.n.</i>	S	58	70	63
<i>Van Berkel 455</i>	NBG	55	65	60
<i>Van der Walt 1417</i>	STEU 3186	60	74	68
<i>P. appendiculatum</i>				
<i>Leipoldt 4395</i>	BOL	72	82	79
<i>Adamson 1484</i>	BOL	72	82	77
<i>Engelbrecht s.n.</i>	STEU 3238	72	89	85
<i>P. campestre</i>				
<i>Jacot-Guillarmod 8300</i>	STEU 2694	62	74	69
<i>P. nephrophyllum</i>				
<i>Acocks 14178</i>	PRE	59	66	62
<i>Walters 123</i>	STE	56	71	63

Table 5.3 (Continue)

Taxon Specimen	Herbarium number	Pollen measurements		
		Min	Max	x (μm)
<i>P. nephrophyllum</i> (Continue)				
<i>Schonken 35</i>	STEU 1531	61	69	64
<i>Snijman 593</i>	STEU 3229	59	71	65
<i>P. carneum</i>				
<i>Van der Walt s.n.</i>	STEU 1653	72	96	82
<i>Van der Walt s.n.</i>	STEU 1654	70	84	77
<i>Coutnik s.n.</i>	STEU 3201	79	89	84
<i>Marais 154</i>	STEU 3492	70	84	78
<i>P. radiatum</i>				
<i>Van der Walt 970</i>	STEU 2114	72	89	81
<i>Van der Walt 1058</i>	STEU 2439	72	84	79
<i>Van der Walt 1063</i>	STEU 2443	72	86	79
<i>Van der Walt 1494</i>	STEU 3476	72	82	78
<i>P. nummulifolium</i>				
<i>Watson 71</i>	STEU 3954	60	91	73
9. LUTEOLUM GROUP				
<i>P. luteolum</i>				
<i>Van der Walt s.n.</i>	STEU 1641	53	60	57
<i>Lavranos 19837</i>	STEU 3054	53	62	58
<i>P. gracillimum</i>				
<i>Marais 161</i>	STEU 3499	43	58	52
<i>Marais 162</i>	STEU 3500	46	53	50
10. RAPACEUM GROUP				
<i>P. rapaceum</i>				
<i>Marais 97</i>	STEU 3394	53	65	58
<i>Marais 322</i>	STEU 3877	55	65	59
<i>Marais 378</i>	STEU 4072	55	70	63
<i>Weber 1</i>	STEU 4078	58	72	65
11. AURITUM GROUP				
<i>P. auritum</i> v <i>auritum</i>				
<i>Van der Walt 482</i>	STEU 556	55	65	61
<i>Marais 96</i>	STEU 3393	48	65	57
<i>Marais 138</i>	STEU 3477	58	65	61
<i>P. auritum</i> v <i>carneum</i>				
<i>Van der Walt s.n.</i>	STEU 1688	50	65	60
<i>Van der Walt s.n.</i>	STEU 1695	55	70	62
<i>P. bubonifolium</i>				
<i>Van Jaarsveld 4230</i>	STEU 2370	55	60	58
<i>Drijfhout 2971</i>	STEU 2886	55	67	58
<i>Drijfhout 2970</i>	STEU 2895	58	62	60

Table 5.3 (Continue)

Taxon Specimen	Herbarium number	Pollen measurements		
		Min	Max	x (μm)
<i>P. parvipetalum</i>				
<i>Bruyns 1519</i>	STEU 1455	58	67	61
<i>Stirton 9242</i>	STEU 3066	55	65	59
<i>Le Roux s.n.</i>	STEU 3240	55	65	60
<i>Marais 327</i>	STEU 3882	46	65	56
<i>P. leipoldtii</i>				
<i>Walters 2</i>	STEU 2986	53	65	59
<i>Muller 4038</i>	STEU 3464	58	67	63
<i>Marais 207</i>	STEU 3640	53	62	58
<i>Marais 317</i>	STEU 3871	58	67	62
<i>P. ellaphieae</i>				
<i>Marais 193</i>	STEU 3618	55	65	60
<i>Marais 197</i>	STEU 3630	55	62	59
<i>Marais 204a</i>	STEU 3637a	53	65	58
<i>Van der Walt 1520</i>	STEU 3734	53	70	61
<i>P. asarifolium</i>				
<i>Hugo s.n.</i>	STEU 862	55	67	61
<i>Van der Walt 573</i>	STEU 864	58	67	62
<i>Ward-Hilhorst 113a</i>	STEU 1350	55	65	59
<i>P. dipetalum</i>				
<i>Marais 170</i>	STEU 3545	58	72	66
<i>Marais 173</i>	STEU 3548	55	65	60
<i>Van der Walt 1525</i>	STEU 3749	62	84	76
<i>Beyers s.n.</i>	STEU 4037	65	77	70
<i>P. ternifolium</i>				
<i>Drijfhout 1627</i>	STEU 855	60	70	64
<i>Van der Walt s.n.</i>	STEU 2200	58	70	64
<i>Marais 164</i>	STEU 3517	58	72	65
<i>Marais 337</i>	STEU 3914	58	67	64
12. TRIPHYLLUM GROUP				
<i>P. triphyllum</i>				
<i>Esterhuysen 18020</i>	BOL	52	66	60
<i>Cillie s.n.</i>	STEU 3838	62	76	68
<i>Von Willert s.n.</i>	STEU 4096	59	74	65
13. CAROLI-HENRICI GROUP				
<i>P. githagineum</i>				
<i>Lavranos 20785a</i>	STEU 3220a	67	77	72
<i>Marais 143</i>	STEU 3482	60	79	68
<i>Marais 243</i>	STEU 3678	58	77	69
<i>P. caroli-henrici</i>				
<i>Bayer 2209</i>	NBG	48	65	55
<i>Drijfhout 2708</i>	STEU 2889	53	65	59
<i>Marais 130</i>	STEU 3427	53	67	62
<i>Marais 281</i>	STEU 3718	58	70	64

Table 5.3 (Continue)

Taxon Specimen	Herbarium number	Pollen measurements		
		Min	Max	x (μm)
<i>P. rubiginosum</i>				
<i>Van Jaarsveld 4100</i>	STEU 2371	48	58	53
<i>Drijfhout 2811</i>	STEU 2888	53	67	62
14. PUNCTATUM GROUP				
<i>P. oblongatum</i>				
<i>Herre s.n.</i>	BOL	72	84	79
<i>Dregè s.n.</i>	OXF	67	82	73
<i>Van der Walt s.n.</i>	STEU 819	72	84	78
<i>P. curviandrum</i>				
<i>Hall 2117</i>	NBG	67	84	76
<i>Barker 65</i>	BOL	67	79	74
<i>Lavranos 20941</i>	STEU 3214	65	79	73
<i>Marais 168</i>	STEU 3543	67	84	75
<i>P. triandrum</i>				
<i>Van der Walt s.n.</i>	STEU 1464	67	91	80
<i>Van der Walt s.n.</i>	STEU 1477	67	74	72
<i>Van der Walt 1276</i>	STEU 2947	62	79	70
<i>Van Niekerk s.n.</i>	STEU 3627	72	91	85
<i>P. punctatum</i>				
<i>Fischer 34</i>	STEU 1578	55	60	57
<i>Van der Walt 944</i>	STEU 2057	58	62	60
<i>Marais 67</i>	STEU 3302	55	60	58

CHAPTER 6

GEOGRAPHICAL DISTRIBUTION, ECOLOGY AND POLLINATION

Information on the ecology of flowering plants is basic to systematics in providing an understanding of the distribution of taxa, the variation within taxa and the adaptations of plants (Jones & Luchsinger 1987). For this study no experimental work in this connection was done, but conclusions were drawn from observations made on collecting trips and in the garden as well as information given on the labels of herbarium specimens.

Although section *Hoarea* is the largest section of *Pelargonium*, it has a rather limited distribution area when compared with some other sections in the genus (Van der Walt & Vorster 1983). It is quite common in the south-western Cape. Goldblatt (1978) regarded the Geraniaceae as one of the characteristic families of the Cape Floristic Region, a statement which is based on the overall presence of *Pelargonium* species in this area. This is not only true for the genus as a whole, but can also be applied for section *Hoarea*. The section also occurs in the other parts of the winter rainfall area along the west coast, that is from the extreme southern part of Namibia, through the Richtersveld and Namaqualand to the Vanrhynsdorp-Calvinia area. It is also found in the southern Cape and as far east as Grahamstown, a region of winter and summer rainfall. A few species occur in the summer rainfall area around Murraysburg and Middelburg in the central Karoo (Figures 6.1 & 6.2).

As previously stated, section *Hoarea* has a relatively small distribution area. Within this limited area at least one species, *P. rapaceum*, has a large distribution area occupying more or less the same area as the section (Figure 8.43.2). On the other hand about twenty percent of the species included in this study have very small distribution areas. This includes species occurring around Nieuwoudtville, Vanrhynsdorp and Clanwilliam, areas with a scant rainfall and at the same time very hot summers. Although Snijman & Perry (1987), in their floristic analysis of the Nieuwoudtville Reserve, did not list any *Pelargonium*, they found this area to be rich in geophytic species, and concluded that geophytes provide the highest proportion of endemic species in the area. As contrasted with the above mentioned species, *P. nummulifolium* occurring at a high altitude and a high annual rainfall, also has a small distribution area. In the eastern Cape there are also species with small distribution areas. In some cases these distributions are based on small numbers of herbarium specimens and could be misleading. In a large number of *Hoarea*

species populations are small with a wide-spread spatial distribution of plants. These plants are usually very difficult to find.

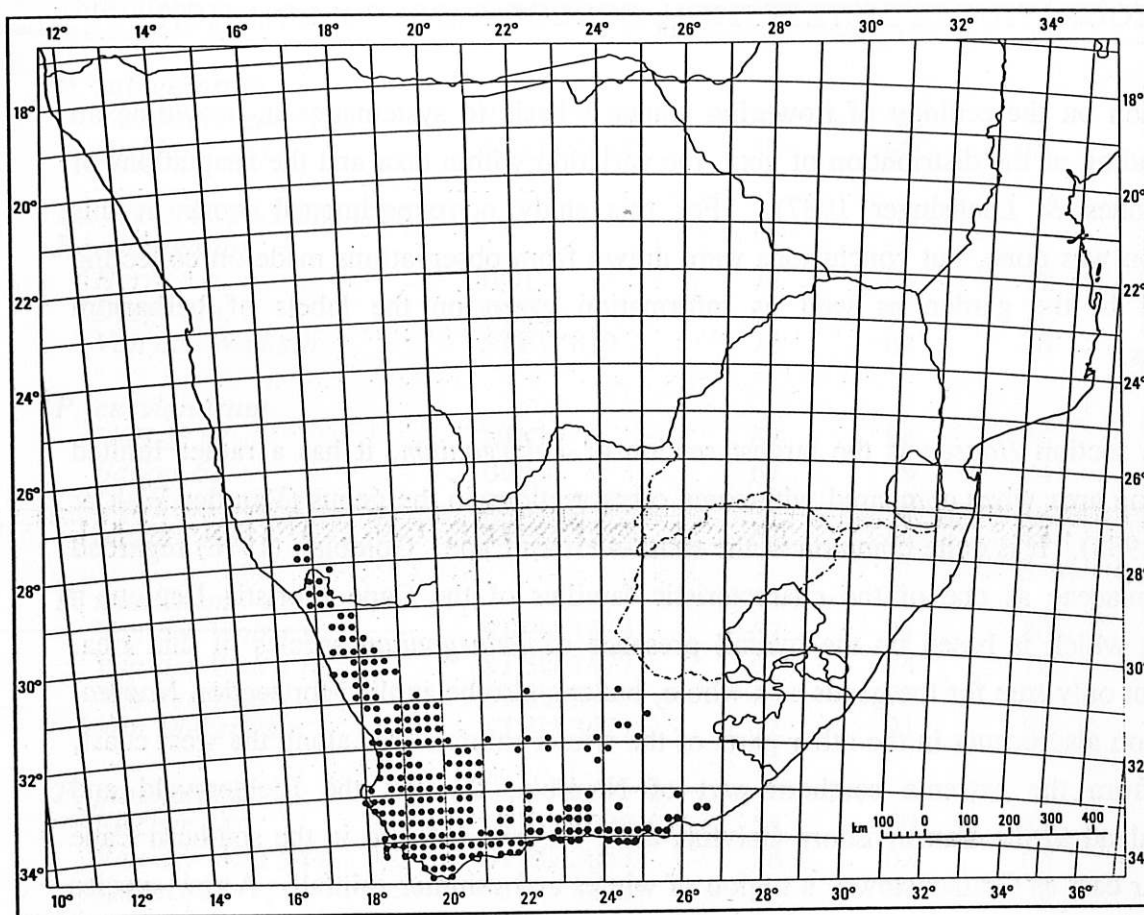


Figure 6.1 Geographical distribution of section *Hoarea*.

The centre of diversity for this section occurs in the one degree square including the town of Worcester (Figure 6.2). This coincides with the centre of diversity of most of the sections of *Pelargonium* and of the genus as a whole (Van der Walt & Vorster 1983). A secondary centre of diversity occurs in the Springbok area, south of the Gariiep element as nominated by Nordenstam (1966). From Vanrhynsdorp to the north there is a decline in the number of species, but this number increases again in the Springbok area. This reduction in the number of species occurring in the Kamiesberg area, could possibly be due to a poor herbarium record of this area, which I doubt it to be, because the Kamiesberge is a very popular collecting area for most botanists, and secondly other taxa like the genera and subgenera of the Mesembryanthemaceae and the species of *Crassula* L. show a similar pattern (Jürgens 1991).

The Springbok area is a region with a very low annual rainfall, dry and hot summers and could be regarded as a semi-desert, and thus regarded as a centre of diversity in

accordance with Raven and Axelrod's (1974) idea that severe deserts and semi-arid transitional areas are important as centres of plant evolution. Secondly, the variable topography of this area creates a variety of microniches where active speciation could take place and as stated by Diamond (1988) that more complex or variegated structured habitats contain more species than simpler habitats.

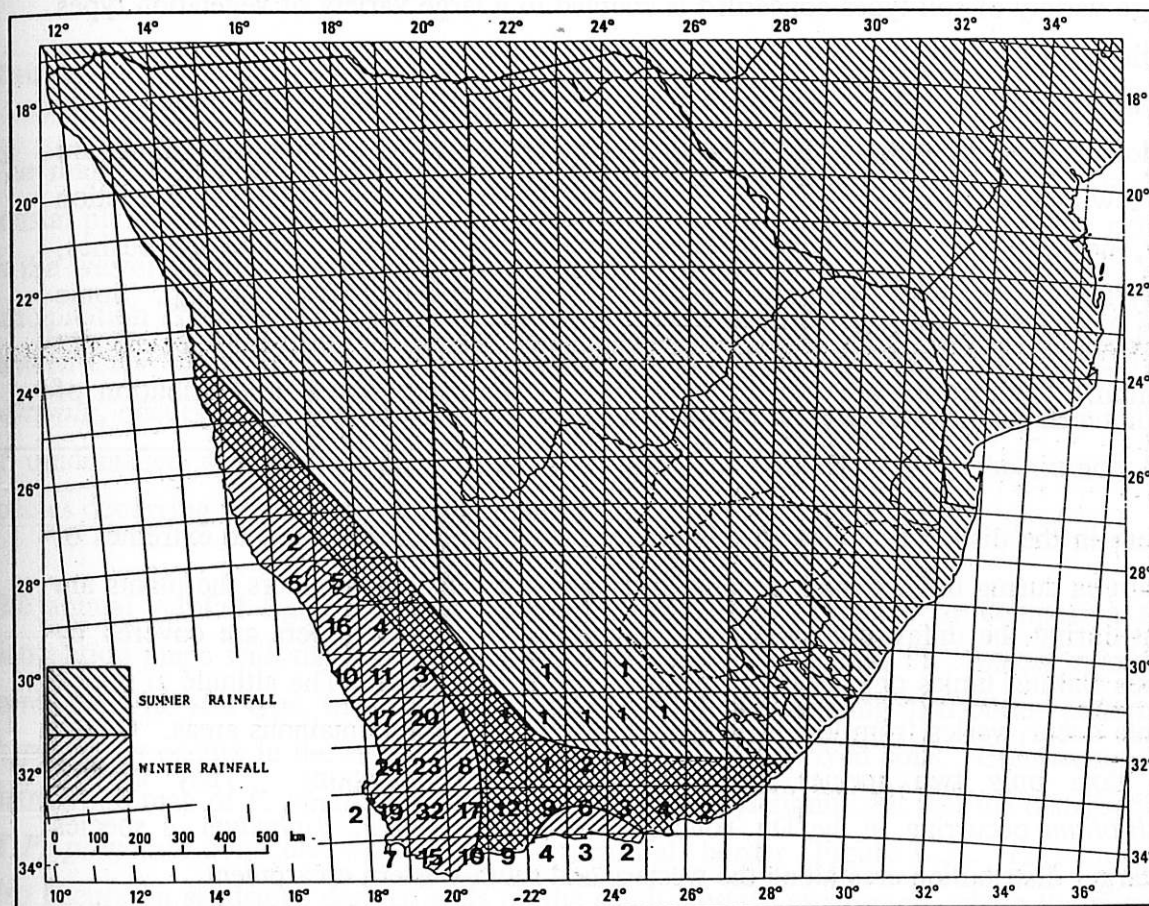


Figure 6.2 Distribution and species diversity of section *Hoarea*.

Like several other sections of the genus *Pelargonium* (*Pelargonium*, *Eumorpha*, *Polyactium* and *Myrrhidium*), with their centre of diversity in the south-western Cape, and with one or more species extending through the summer rainfall region (Van der Walt & Vorster 1983), *Hoarea* has also an extension in the summer rainfall area (Figures 6.1 & 6.2).

Habitat

The majority of species in this section grow in sandstone derived soils, but are seldom restricted to this type of substrate. Several species occur on a wide variety of soils like sand, clay, loam, lime, quartz and weathered granite. Most species of section *Hoarea*

seem not to give preference to specific types of soil, so that I do not regard the substrate alone being an important factor determining the distribution patterns of the species. The annual rainfall plays a more important role in this connection and a combination of substrate and rainfall should be considered as a determining factor in the distribution patterns.

The large variety of soil types concerned is coupled to a large variety of vegetation types in which species of this section occur. Although most species occur in fynbos, they usually are not restricted to it and renosterveld and different types of succulent or karroid vegetations create also suitable habitats for them. Succulent or karroid vegetations are usually low and open ones in which most plants are exposed to direct sunlight. In section *Hoarea*, however, the majority of species occur in rock crevices and under bushes, probably because these are the only niches in which they survive heavy grazing. Some species occur on plains or flat areas, but mountainous habitats or steep hillsides are not uncommon. Populations are usually small with a wide-spread spatial distribution of plants.

No where in the distribution area of this section, are the plants subjected to extremes of temperatures during the growing season. In areas with very hot summers the plants are dormant during the unfavourable season. Additional to this the tubers are covered by numerous flaking tunics or periderms, which serve as insulators. The altitude at which the plants occur, varies from low elevations near sea level to mountainous areas. Of the studied taxa only two species are restricted to high mountains. They are *P. nummulifolium* occurring in the Du Toitskloof Mountains and *P. triphyllum*, a species with a larger distribution area along the western and south-western escarpment.

No studies of the reaction of these plants to fire were undertaken, but field observations revealed an expected pattern for tuberous plants. Older plants with fire scars sprout again during the next winter. At the same time numerous seedlings occur in the first but also in the second winter after the fire. With further development of the vegetation after the fire the number of individuals declines.

Reproduction by seed is the most important mode for increasing in numbers and keep up capacity levels of the different populations, although in cultivation the division of the tuber could be successful in some cases. However, in *P. fasciculaceum* older plants in the field are found to form colonies in sandy soil (Marais 1991). This is similar to what is found *P. triste* (L.) L'Hérit. of section *Polyactium* and also in different members of section *Campylia* (Van der Walt & Van Zyl 1988). Because of the branching of the

fleshy roots, *P. fasciculaceum* develops an extensive root system with several stem-growing points. In the same area older plants are often found in colonies, whereas younger and smaller plants grow singly. This indicates that in nature plants of *P. fasciculaceum* easily develop from seeds. Although numerous stem divisions were also observed in *P. appendiculatum* and to a lesser extent in *P. triphyllum*, the formation of colonies does not occur in the majority of species in this section.

Rainfall

The majority of species studied occur in the winter rainfall region along the western coastal plain and the western escarpment (Figure 6.2). Six of the 60 taxa studied, occur in the western Cape, where winter rain prevails, but also in the eastern Cape where the precipitation could occur throughout the year. Another three taxa are restricted to the eastern Cape where the precipitation occurs throughout the year. Only one species, *P. aestivale*, occurs in the central Karoo, which is a summer rainfall area. A small number of unidentified specimens, collected in the Karoo, was found. Thus the number of species occurring in the Karoo could be more.

The annual rainfall figures for the different species were compiled by comparing the distribution maps with that of rainfall maps (Jackson 1961, Table 6.1). Annual rainfall, combined with soil type, may play an important role in determining distribution patterns. *P. pinnatum* occurs in the southern Cape on mainly shale derived soils. Comparing the distribution map of *P. pinnatum* with the rainfall map it is significant that the distribution of *P. pinnatum* coincides with the 400 mm rainfall border (Figure 6.3). *P. pinnatum* also occurs on sandstone derived soils on the south-western escarpment where the annual rainfall is much higher (600--1000 mm). The same could account for the distribution patterns of *P. auritum*, *P. rapaceum*, *P. carneum* and *P. dipetalum*, all of them species with large distribution areas, occurring on a variety of substrates in areas with wide ranges in the rainfall figures. The occurrence of *P. chelidonium*, *P. violiflorum* and *P. proliferum* in smaller distribution areas than the above mentioned species, but also with a similar wide range in the rainfall figures, could probably be explained because of the different types of soil in which they occur.

Table 6.1 Annual rainfall figures for the different species of section *Hoarea* (Continue).

Species	0	100	200	300	400	500	600	700	800	900 mm
8. Incrassatum group (Continue)										
<i>P. campestre</i>							—————			
<i>P. nephrophyllum</i>		—————								
<i>P. carneum</i>		—————								
<i>P. radiatum</i>								—————	—————	
<i>P. nummulifolium</i>								—————	—————	
9. Luteolum group										
<i>P. luteolum</i>		—————	—————							
<i>P. gracillimum</i>		—————	—————							
10. Rapaceum group										
<i>P. rapaceum</i>		—————	—————	—————	—————	—————	—————	—————	—————	—————
11. Auritum group										
<i>P. auritum v auritum</i>		—————	—————	—————	—————	—————	—————	—————	—————	—————
<i>P. auritum v carneum</i>		—————	—————	—————	—————	—————	—————	—————	—————	—————
<i>P. bubonifolium</i>	—————									
<i>P. parvipetalum</i>		—————								
<i>P. leipoldtii</i>		—————								
<i>P. ellaphieae</i>						—————	—————			
<i>P. asarifolium</i>						—————	—————			
<i>P. dipetalum</i>				—————	—————	—————	—————			
<i>P. ternifolium</i>							—————	—————	—————	—————
12. Triphyllum group										
<i>P. triphyllum</i>							—————	—————	—————	—————
13. Caroli-henrici group										
<i>P. githagineum</i>		—————								
<i>P. caroli-henrici</i>		—————	—————							
<i>P. rubiginosum</i>		—————								
14. Punctatum group										
<i>P. oblongatum</i>		—————								
<i>P. curviandrum</i>		—————								
<i>P. triandrum</i>		—————								
<i>P. punctatum</i>		—————	—————							

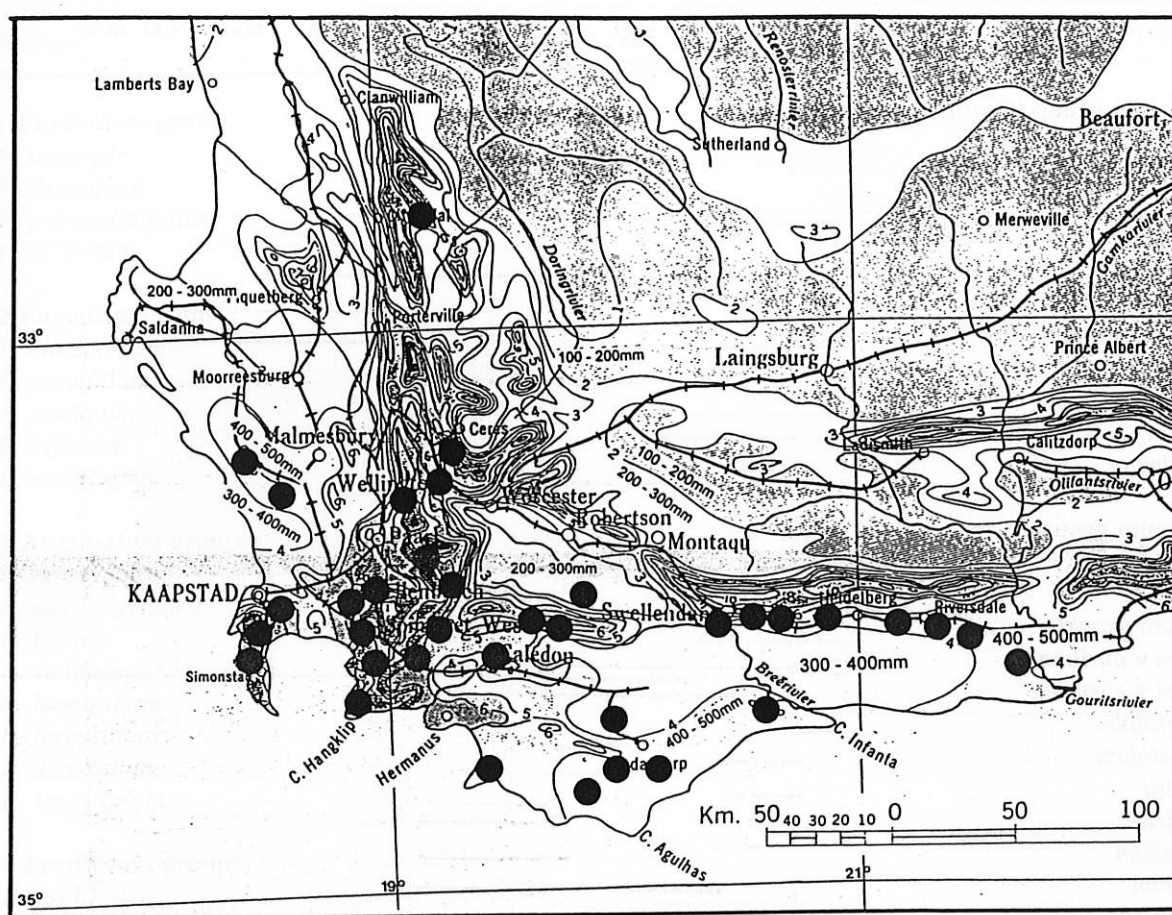


Figure 6.3 A comparison between the distribution of *P. pinnatum* and the annual rainfall figures.

- | | |
|---|---|
| 1 = borderline of the 100 mm rainfall area. | 4 = borderline of the 400 mm rainfall area. |
| 2 = borderline of the 200 mm rainfall area. | 5 = borderline of the 500 mm rainfall area. |
| 3 = borderline of the 300 mm rainfall area. | 6 = borderline of the 600 mm rainfall area. |

In a few cases it seems that presumably related species occupy adjacent distribution areas due to the differences in the rainfall figures. *P. heterophyllum* occurs in an area with an annual rainfall of 300--400 mm, whereas *P. tenellum* occupies an adjacent area with an annual rainfall figure of 400--600 mm. *P. petroselinifolium* occupies an area with an annual rainfall of up to 1000 mm, whereas the presumably related *P. fissifolium* occurs in an adjacent area with an annual rainfall of 200--300 mm. A similar case is that of *P. radiatum*, which occurs in an area with a higher (1000 mm) rainfall figure than that of *P. carneum* (200--800 mm).

The annual rainfall figure may also play an important role in the discontinuous distribution pattern of *P. leptum* (Figure 6.4) and *P. ellaphieae* (Figure 6.5). Both species occur in the Cape Peninsula or the vicinity thereof as well as in the Olifantsrivier Valley and the Cederberge, 150 to 200 km to the north. This distribution pattern

coincides with the annual rainfall of 400--600 mm. I must admit that these conclusions were made on a small number of herbarium specimens and that the extensive cultivation of the Swartland has possibly reduce the chances of founding them there. On the other hand other *Hoarea* species still occur in the small undisturbed patches in this area and that the disjunct distribution patterns of *P. leptum* and *P. ellaphieae* can be ascribed to the annual rainfall of the area.

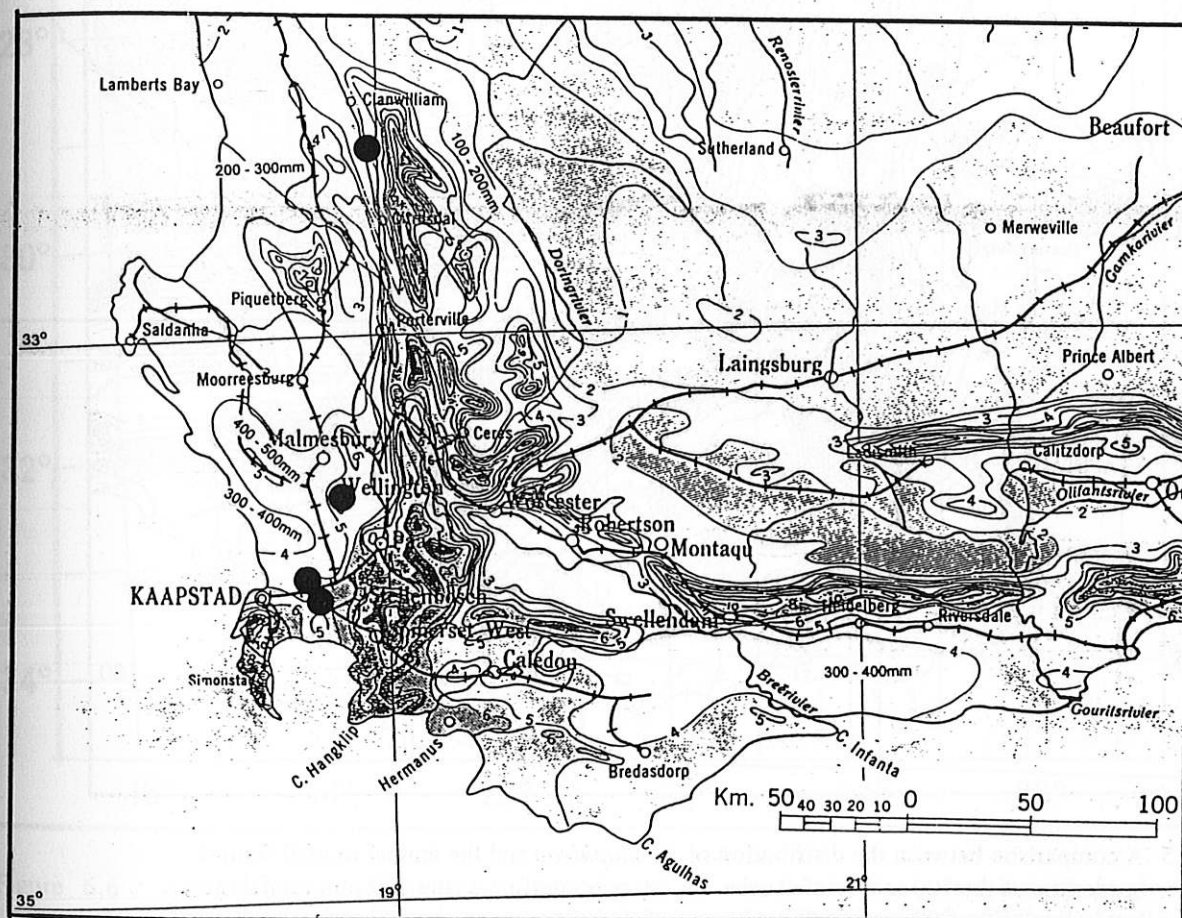


Figure 6.4 A comparison between the distribution of *P. leptum* and the annual rainfall figures.

- | | |
|---|---|
| 1 = borderline of the 100 mm rainfall area. | 4 = borderline of the 400 mm rainfall area. |
| 2 = borderline of the 200 mm rainfall area. | 5 = borderline of the 500 mm rainfall area. |
| 3 = borderline of the 300 mm rainfall area. | 6 = borderline of the 600 mm rainfall area. |

Six of the 59 species studied occur in areas with a high annual rainfall (600--1000 mm). Two of them, *P. nummulifolium* and *P. triphyllum*, are restricted to high altitudes. The other four, *P. radiatum*, *P. ternifolium*, *P. longifolium* and *P. trifoliolatum*, occur on high mountains, but also on low land flats with a relatively high annual rainfall (Table 6.1). Sixteen species occur in areas with an annual rainfall of less than 200 mm and

another 14 species occur in areas where the rainfall varies between 100--300 mm per annum. Thus fifty percent of the species studied occurs in areas with an annual rainfall of less than 300 mm (Table 6.1). From this I conclude that rainfall plays an important role in the distribution patterns of *Hoarea* species, and might be one of the major driving forces of speciation in this section.

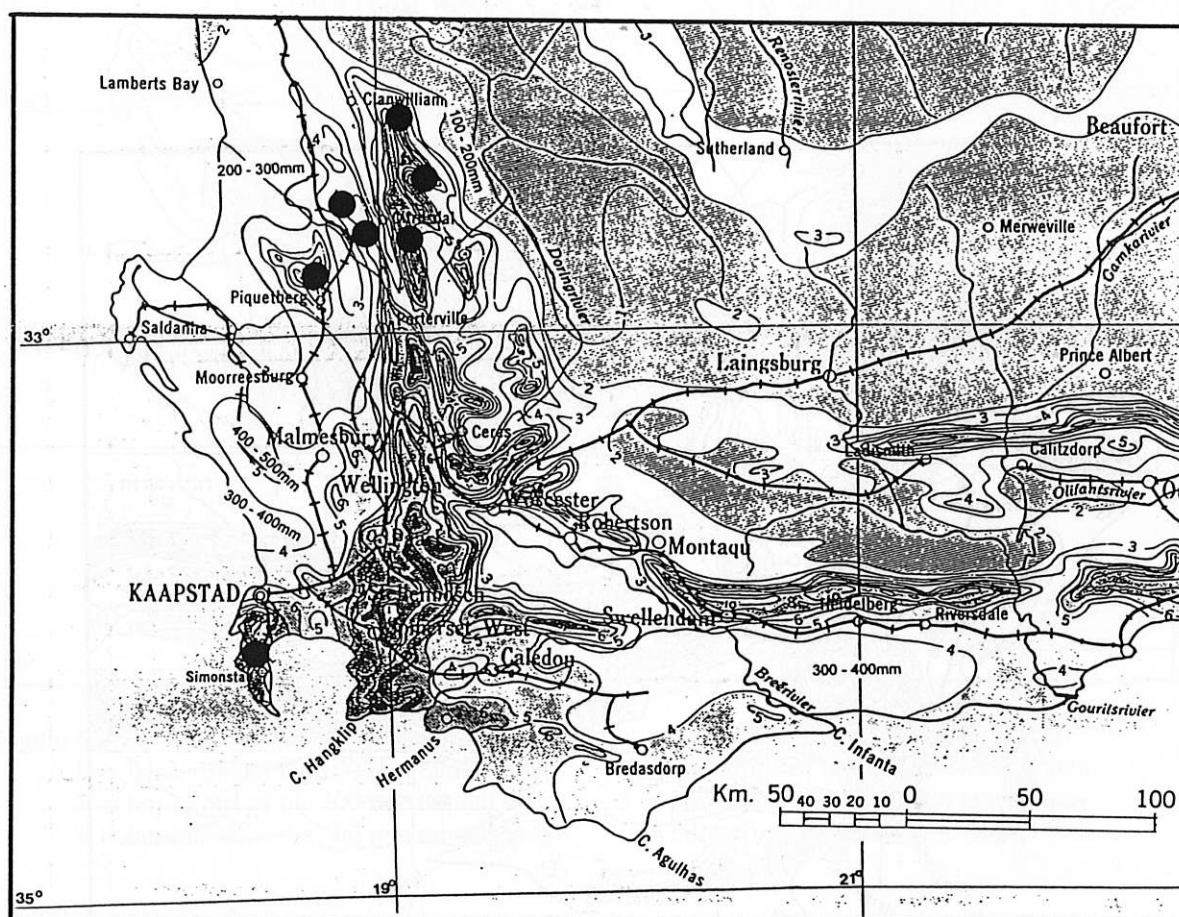


Figure 6.5 A comparison between the distribution of *P. ellaphiae* and the annual rainfall figures.

- | | |
|---|---|
| 1 = borderline of the 100 mm rainfall area. | 4 = borderline of the 400 mm rainfall area. |
| 2 = borderline of the 200 mm rainfall area. | 5 = borderline of the 500 mm rainfall area. |
| 3 = borderline of the 300 mm rainfall area. | 6 = borderline of the 600 mm rainfall area. |

Flowering time

The section *Hoarea* is represented by deciduous geophytes most of which flower in summer after the leaves have been shed. The plants remain dormant during the unfavourable season and sprout after the first rains of the next growing season. In the majority of species the apical meristems of the stems are protected during dormancy by a dense crown of petiole remains. In the winter rainfall area the leaves appear from April

to June, after the first winter rains, and in the summer rainfall area, after early spring showers or any rain following a drought.

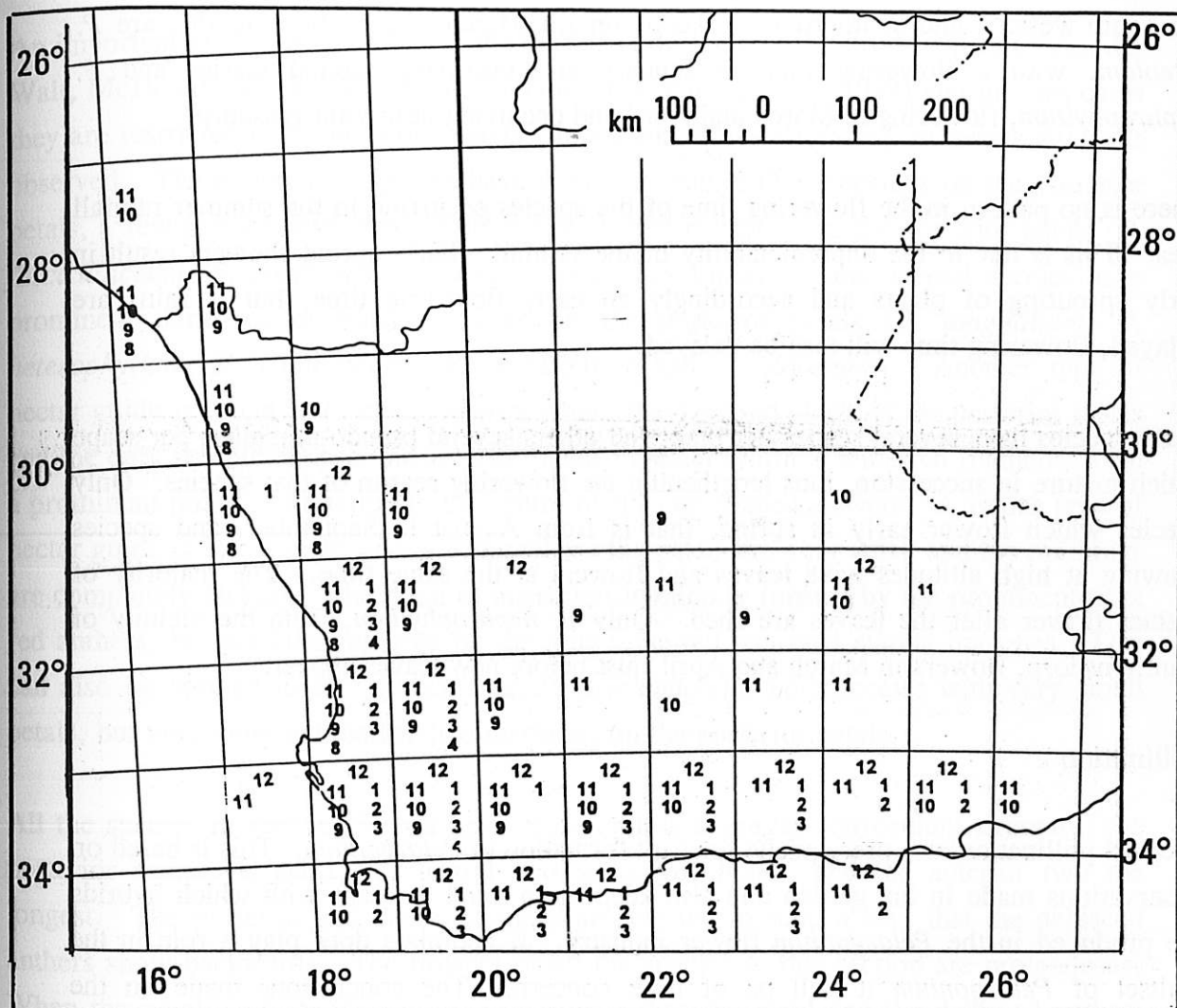


Figure 6.6 An illustration of the flowering time of all *Hoarea* species occurring in a given latitude/longitude square. 1 = January, 2 = February, 3 = March, 4 = April, 8 = August, 9 = September, 10 = October, 11 = November, 12 = December.

The flowering time for this section starts during August and keeps on till March and April, with the peak during October and November. From herbarium specimens the flowering time of all species occurring in a latitude/longitude square was determined (Figure 6.6). According to Figure 6.6 the flowering time starts in August along the coast of Namaqualand and inland species flower at a later stage. Moving south, flowering time starts later and moving east, this is still later. This is in accordance with the peak of the flowering time for the different regions. In Namaqualand the peak of the flowering time is the end of August or beginning of September, in the south-west Cape it is late September and in the southern Cape it is October. However, if the flowering times for

the different species are considered, the peak of the flowering time for the majority of species of *Hoarea* for every latitude/longitude square, is later than that of the rest of the vegetation. This pattern also shows that the flowering time for *Hoarea* species in Namaqualand is from August to November, whereas the flowering time of the species in the south-western and southern Cape keeps on till March. Exceptions to this are *P. luteolum*, with a flowering time in January and occurring around Garies and *P. nephrophyllum*, flowering in March and April and occurring near Vanrhynsdorp.

There is no pattern in the flowering time of the species occurring in the summer rainfall area. This is due to the unpredictability of the rainfall. Early spring showers result in early sprouting of plants and accordingly an early flowering time, but if rains are delayed, flowering time will also be delayed.

Some species have several scapes per plant and others several pseudo-umbellets per scape which mature in succession, thus lengthening the flowering season of that species. Only species which flower early in spring, that is from August to September, and species growing at high altitudes have leaves and flowers at the same time. The majority of species flower after the leaves are shed. Only *P. nephrophyllum*, from the vicinity of Vanrhynsdorp, flowers in March and April, just before new leaves appear.

Pollination

I regard pollination as a prerequisite for fruit formation in *Pelargonium*. This is based on observations made in the garden and also keeping in mind the ease with which hybrids are produced in the *Pelargonium* flower industry. If apomixis does play a role in the fruitset of *Pelargonium* it will be of little concern. The conclusions made on the pollination biology of section *Hoarea* are based on the success of fruit formation in the different species.

The majority of species of *Pelargonium* are probably entomophilous. Bees and other insects are often found visiting the flowers of *Pelargonium* and several authors referred to insects visiting *Pelargonium* flowers (Scott Elliot 1891, Burkhill 1899, Vogel 1954, Van der Walt, McDonald & Van Wyk 1990, McDonald & Van der Walt 1992, Zietsman 1993). This can also be extrapolated to section *Hoarea*.

Regarding the different factors influencing pollination vectors, only two species, *P. ellaphieae* and *P. grenvilleae*, of section *Hoarea* have strongly scented flowers. *P. appendiculatum* is an aromatic geophyte, but this is probably due to volatile oils excreted

by the leaves or by the whole plant, and not an attractant or odour which is observed only during anthesis. Like all *Pelargonium* species, the flowers of all *Hoarea* species produce nectar, but in this study no analyses were performed on it.

An important attraction to insects is the markings or nectar guides on the petals (Van der Walt, McDonald & Van Wyk 1990, McDonald & Van der Walt 1992) and in most cases they are restricted to the posterior petals. In section *Hoarea* a variety of nectar guides is observed. The majority of species have wine-red feather-like markings on the posterior petals, a few species have dimly coloured V-shaped markings on the posterior petals (*P. fasciculaceum*, *P. connivens*, *P. luteum* and *P. fumariifolium*) and several species have prominent dark red or black blotches on the posterior petals (*P. longifolium*, *P. heterophyllum*, *P. trifoliolatum*, *P. moniliforme* and *P. vinaceum*). Another type of nectar guide is found in *P. caroli-henrici* where the dark red claws of the posterior petals and the dark red blotches on the anterior petals together with the wine-red filaments form a prominent point of attraction in the centre of the cup-shaped flowers. A fourth type of nectar guide is found in *P. githagineum* where the petals are very small and the markings are completely lacking. The point of attraction is initially formed by the prominent dark red anthers, but are later replaced by the long wine-red recurved stigma branches. This can also be applied to *P. leipoldtii* and *P. parvipetalum*, both species with very small petals, but with wine-red feather-like markings on the posterior petals.

All the species in section *Hoarea* have more or less a similar androecium structure, the posterior stamen is short, the lateral two somewhat longer and the anterior two the longest. The posterior and lateral stamens are twisted in such a way that the dehiscent anthers show backwards. The flowers of all the species in this section are protandrous. When the petals unfold, the stamens are longer than the pistil and the dehiscent anthers are borne in a way to form a flat pollen-covered surface which must be touched by the abdomen of the insect visiting the flowers (Scott Elliot 1891). During anthesis the pistil lengthens and the style bends upwards, while the stigma branches recurve, occupying the original position of the anthers. At the same time the filaments bend downwards and in most cases the anthers are dropped, a mechanism to avoid self-pollination. Exceptions to this are *P. caroli-henrici* where the free filaments are twisted so that pollen surfaces are turned to the front, *P. luteum* where the filaments are twisted in an unique way, forming a pollen-lined tunnel to the nectar tube (Figure 8.28.2), and *P. fumariifolium* with a similar androecium than *P. luteum*, but with only two fertile stamens.

For the majority of species fruitset under cultivated conditions is rare. Hemsley and Ferguson (1985) stated that it is not necessary for plants to be optimally adapted with

respect to all of its morphological features, because an inefficient pollination system may be compensated for by great longevity. This could be true for section *Hoarea*, but field collections and herbarium specimens reveal that fruit formation under field conditions is usually very successful. The poor fruitset in the garden could probably be ascribed to the variation in the structure of the androecium of the different species and in most cases a special adapted structure which is dependent on a special pollinator, and this pollinator is not present in the garden.

In species with very long curved stamens, like *P. punctatum* and *P. oblongatum*, fruitset in cultivation is poor, but in field collections, every flower was found to produce a mericarp. This implies that in nature there is no imperfection in the reproductive biology of these species. Hand-pollination applied in the garden to the flowers of *P. oblongatum* results in complete fruitset in the case of cross-pollination, but was less successful in self-pollination.

Fruitset in cultivation of *P. auritum*, *P. bubonifolium* and *P. parvipetalum* is very successful. In all three species the five fertile stamens are more or less of the same length and protrude from the flower. All three species flower in spring, that is from August to October. In *P. asarifolium* and *P. ellaphieae*, species with a similar androecium than the above mentioned three, fruitset in the garden is poor. These two species flower in summer, that is from November to March. Two possibilities for this behaviour could be considered. As self-compatibility is not uncommon in *Pelargonium* (*P. candicans* Spreng, Marais 1981; *P. dolomiticum* Knuth, Zietsman 1993; *P. oblongatum*, own observations), this could be the case for *P. auritum*, *P. bubonifolium* and *P. parvipetalum*. Although the flowers are protandrous, the differences in the time of ripening of the anthers and that of the stigmas could be very short, and self-pollination in these cases could be very successful, which is not the case of the second group. A second possibility is that a suitable pollinator is present in the garden during spring, but not during summer.

A similar observation was made in *P. appendiculatum*, an early flowering species, and that of *P. radicum*, which flowers during summer. The floral structures of the two species are very similar. Fruitset in the garden in *P. appendiculatum* is very successful, but not so in *P. radicum*.

Although it seems that flowers with very short stamens together with very short pistils, concealed in the floral sheath, could create an ideal situation for self-pollination, this is

not true for *P. pinnatum* and *P. nervifolium*. Fruitset in the garden of these species is not very successful; only one or two mericarps per pseudo-umbellet are formed.

Although the basic structure of the androecium is very similar in all the species of *Hoarea*, the relative length of the stamens is diagnostic at specific level. The length of the stamens varies from much shorter than, the same length as or longer than the calyx. This results in different types of floral structures, which could be regarded as a co-evolution for the pollination strategy. For that reason the pollination biology of section *Hoarea* could be one of the more important driving forces in the evolution of this section, resulting in the large diversity in the length of the stamens and the way the stamens are borne during anthesis.

CHAPTER 7

DISCUSSION AND CONCLUSION

Section *Hoarea* is a very large section, demarcated by characteristic turnip-shaped, elongated and often moniliform tubers with smooth flaking periderms. The growth form delimits the section as a natural taxonomic unit (Marais 1989a), and within this unit there exists a large variation in the floral structure.

Hoarea as a section of *Pelargonium*

Previous studies in *Pelargonium* indicated little relationship between the floral structure of section *Hoarea* and that of the rest of the genus (Marais 1981). Secondly, no natural hybrids between any of the *Hoarea* species and species of any other section of *Pelargonium* exist, whereas natural hybridization between species of different sections in *Pelargonium* does occur (Van der Walt 1985, Gibby & Westfold 1986, Albers & Van der Walt 1992). The question arises whether *Hoarea* ought to be included in *Pelargonium*, or whether it should be a genus on its own as was proposed by Sweet (1820). Therefore the basic structure of the flowers of all sections in *Pelargonium* was compared to that of *Hoarea*.

In *Pelargonium* flowers are borne in pseudo-umbels, with several flowers per inflorescence (Marais 1981). In section *Hoarea* the flowers are borne on a scape, which is usually branched, bearing several pseudo-umbellets per scape. In both cases the older flowers are in the centre and the buds on the periphery, and can be described as an umbelliform dichasium (Wyatt 1982).

The presence of a hypanthium in all *Hoarea* species is also typical for the genus. In *Hoarea* the hypanthium is long (6--100 mm) in comparison with the very short pedicel (0,5--1 mm), and the hypanthium length/pedicel length ratio equals the length of the hypanthium. This ratio remains constant for *Hoarea*. In the rest of the genus, the hypanthium length/pedicel length ratio does not vary only among the different sections of *Pelargonium*, but also within the different sections (Marais 1981) and can be used as a diagnostic tool to differentiate between species.

The morphology of the sepals of all *Hoarea* species is very similar to that of the rest of the genus. In all *Pelargonium* species the sepals are persistent, covering the basis of the

developing fruit, and in all species of the genus the sepals are of little or no taxonomic value (Marais 1981).

Like all the species in the rest of the genus, *Hoarea* species also have zygomorphic flowers. In all species a difference occurs in the form and the size of the posterior two petals and that of the anterior three. The degree of zygomorphy is emphasized by the differences between the orientation of the posterior petals and those of the anterior three.

The basic structure of the androecium in all *Pelargonium* species is the same. It consists of ten filaments, arranged in two whorls of five each, basally connate, and obdiplostemonous (Figure 3.2). The androecium is zygomorphic; the staminal column is longer on the posterior side than on the anterior one, and the anterior stamens are longer than the posterior one. The staminodes are usually very short. In most species the posterior and lateral stamens are twisted in such a way that the dehiscent anthers show backwards, forming a flat pollen-covered surface which must be touched by the abdomen of the insect visiting the flowers (Scott Elliot 1891). The length of the stamens in section *Hoarea* varies from shorter than, the same length as or much longer than the sepals. This represents the same spectrum of variation that occurs in the different sections of *Pelargonium* (Marais 1981). The number of fertile stamens in *Pelargonium* varies from two to seven (Table 3.5). This variation could be used as a diagnostic tool, or in some sections it confirms relationship between species.

The structures of the gynoecium and the fruit in *Hoarea* species, are typical for the genus, and the variation in the length of the style and the rostrum represents the same variation that exists in the genus.

The leaf anatomy of section *Hoarea* corresponds well with the rest of the genus (Volschenk 1980, Van der Walt & Boucher 1986, Maggs 1987, Van der Walt & Van Zyl 1988, Dreyer 1990b, Marais 1990b, Scheltema & Van der Walt 1990). The leaves are amphistomatic and the stomata anomocytic. Both dorsiventral and isobilateral leaves occur in sections *Pelargonium* (Volschenk 1980), *Myrrhidium* (Van der Walt & Boucher 1986), *Campylia* (Van der Walt & Van Zyl 1988), *Jenkinsonia* (Scheltema & Van der Walt 1990), *Ligularia* (Marais 1990b), *Cortusina sensu stricto* and *Reniformia* (Dreyer 1990b), and often closely related taxa can be distinguished because of the dorsiventral or isobilateral leaves. The same accounts for the presence or absence of a medullary bundle in closely related species.

The pollen morphology of *Hoarea* fits in well with that of the genus. The pollen grains are spherical, radiosymmetric, isopolar, tricolporate monads. The pattern of the tectum varies from reticulate, reticulate-striate, striate-reticulate, to striate. In *Hoarea* an extremely striate pattern of the tectum occurs that does not occur in any other section of *Pelargonium*. On the other hand a double structure of the tectum occurs in section *Polyactium* (Marais 1981, Verhoeven & Marais 1990), and a reticulate tectum with minute luminae occurs in *Ligularia* (Verhoeven & Marais 1990, Van der Walt, Albers & Gibby 1990), which does not occur in *Hoarea* or the other sections of *Pelargonium*. The size of the pollen grains of *Hoarea* (equatorial diameter 43--95 μm) coincides with that of the whole spectrum of *Pelargonium*.

The presence of a hypanthium, the morphology of the sepals, the difference in the form and size of the posterior and the anterior petals, the basic structure of the androecium, and the similarities in the structure of the gynoecium, are characteristics present in all *Pelargonium* species and also present in all *Hoarea* species. The variations of these features in *Hoarea*, represent the same spectrum of variations occurring in the genus. The variations in the leaf anatomy and the pollen morphology also fit in well with the rest of the genus. Although no natural hybrids between *Hoarea* species and species of any other section of *Pelargonium* exist, crossings under cultivated conditions could be enforced (De Marie, personal communication) and although the floral structure of *Hoarea* shows apparently little relationship with the rest of the genus, the basic structures of the flowers that demarcate other sections as part of *Pelargonium*, are also present in *Hoarea*. Therefore I regard *Hoarea* as a well defined section within *Pelargonium*.

The position of section *Hoarea* in the genus

Section *Hoarea* does not represent the only tuberous species in *Pelargonium*, but the subterranean flaking tuber with the short flattened stem, from which leaves and a scape emerge is distinctive for the section and is unique for *Pelargonium*. The tuber in *Hoarea* is a root and the peeling tunics or periderms are smooth, giving the tuber a smooth surface. This is in contrast with other tuberous species in *Pelargonium*. Although the tubers in sections *Polyactium* and *Reniformia* (Dreyer 1990b) are also fleshy roots they do not produce smooth, flaking periderms, instead, the tubers develop more persistent periderms with scurfy surfaces. Several members of sections *Campylia* (Van der Walt & Van Zyl 1988) and *Polyactium* are soboliferous, and in *Polyactium* the underground stems are also fleshy, and in appearance very similar to the fleshy roots. The short flattened stem of section *Hoarea* produces leaves, arranged in a rosette, and a scape without leaves. Tuberous species of section *Polyactium* produce short epigeal stems

with leaves and flowering stems. Although the tubers in the different sections of *Pelargonium* are fleshy roots they are not identical in all sections and have probably originated at different times in different groups.

The long curved stamens of the *Punctatum* group are very similar to those of section *Jenkinsonia* (Marais 1981), and likewise is the androecium of the *Auratum* group similar to that of section *Otidia* (Marais 1981). However, in *Otidia* the staminal column is not papillate. Both these cases I regard as convergent evolution in reaction to the pollination strategies of the different groups. Another example of convergent evolution is the large stipules of *P. appendiculatum*, which are similar to those of *P. stipulaceum* (L. f.) Willd. of section *Ligularia*.

Section *Hoarea* seems to be well defined in respect to growth form. At the same time the floral morphology reveals a large variety in structure. This is similar to section *Campylia*, which is demarcated by a caespitose type of growth form, but at the same time represents a considerable variation in floral structure (Van der Walt & Van Zyl 1988). In respect to morphological characters no close relationships between section *Hoarea* and any other section of the genus could be traced.

The subdivision of section *Hoarea*

Although the morphology of the tuber of *Hoarea* is a distinctive character by which the section is demarcated from the rest of the genus, the morphology of the tuber is of little or no taxonomic value within the section itself. A large variation in leaf shape occurs within the section. If only leaf form is considered, twelve different forms are recognized (Figure 3.1). If the leaf texture, indumentum and incisions are also considered, some of the major groups are subdivided into smaller groups (Figure 3.1). Comparing floral morphology to leaf form, it confirms Dickison's (1975) statement that evolutionary modifications of vegetative characteristics are not necessarily closely synchronized with floral evolution (Table 3.6). Leaf form suggests relationship in the *Aciculatum* group and also in the *Punctatum* group, but in the majority of floral groups leaf form can be used to distinguish between species.

One of the diagnostic characters of the section is the stipules which adnate to the petioles. In the majority of species the stipules are long and subulate. In species with prostrate leaves the stipules are usually short and triangular. Only in *P. appendiculatum* the shape of the stipules is a diagnostic character within section *Hoarea*.

In the majority of species in *Hoarea* flowers are borne on a branched scape, forming a compound inflorescence. Two thirds of the species have less than fifteen flowers per pseudo-umbellet. This includes all the species with very short stamens (Table 3.1, *Fissifolium*, *Pinnatum*, *Attenuatum* and *Proliferum* groups), and the *Heterophyllum* and *Auratum* groups. Some species in the other groups also have small numbers of flowers per pseudo-umbellet, where this character acts as a diagnostic feature. However, its diagnostic value is lessened by the large variation that could occur in several species (Table 3.1).

The very long hypanthium, together with the very short pedicel is diagnostic for the section. Within the section a short hypanthium demarcated the *Auratum*, *Luteum*, *Proliferum* and the *Heterophyllum* groups. On the other hand this feature can be a diagnostic character to differentiate between closely related species (Table 3.2).

The majority of species have five-petalled flowers. *P. triandrum* is the only species with only four petals, in which case it is a diagnostic character. Five species, *P. leipoldtii*, *P. ellaphieae*, *P. asarifolium*, *P. dipetalum* and *P. ternifolium* have two-petalled flowers. The androecium of these five species is very similar and the reduction in the number of petals confirms relationship amongst these species.

Although the majority of species in *Hoarea* have dull-coloured flowers, there are species with bright colours and in these cases flower colour could be a diagnostic feature (*P. incrassatum* versus *P. grenvilleae*, *P. auratum* var. *auratum* versus *P. auratum* var. *carneum*, and *P. petroselinifolium* versus *P. fissifolium*). The presence of pollinator guides is common in *Pelargonium*. The form and size of the guides could be a diagnostic feature (*P. heterophyllum* versus *P. tenellum*), or it can confirm a relationship between species (*P. heterophyllum* and *P. trifoliolatum*).

The form and the size of the petals, and the length/width ratio of the posterior petals play an important role in the delimitation of smaller groups within *Hoarea*. In flowers with very short stamens this ratio is important for demarcating smaller groups.

The relative length of the stamens in section *Hoarea* is diagnostic at specific level and varies from much shorter than, the same length as or longer than the sepals. Different modifications of the flowers contribute to the reproductive success of a species (Jones & Luchsinger 1987). In the case of *Hoarea* the structure of the androecium plays a major role in this process. Variation in the structure and especially the length of the stamens and the way in which they are borne determine the success for pollination. The poor

fruit formation under cultivated conditions indicates that pollinators are absent in the garden. Thus, special pollinators are needed for special structures of the androecium. For that reason the subdivision of the section was based on the length of the stamens in relation to that of the sepals, and secondly the length of the anterior stamens in relation to those of the lateral and the posterior ones. Additionally to this the structure of the pollen tectum (Table 5.2) and the size of the petals, as well as the length/width ratio of the posterior petals (Table 3.4) were considered in constructing the subdivision. Other external morphological structures were also considered. Chromosome numbers only influenced my decision on demarcating *P. aestivale*, *P. fissifolium*, *P. petroselinifolium* and *P. aristatum* as a separate group. According to Albers (personal communication), these four species have a basic chromosome number of $x = 9$, which is an unusual basic number for section *Hoarea*. This can be considered as a derived chromosome number since the primitive basic number for *Pelargonium* is $x = 11$ (Albers & Van der Walt 1984). The external morphology of these four species was studied for characters to confirm close relationships among them. All four species have very short stamens, less than 20 flowers per pseudo-umbellet, and a similar structure of the pollen, thus morphological evidence to justify their clustering in the *Fissifolium* group. On the other hand, if petal morphology is considered, three of the species (*P. aestivale*, *P. fissifolium*, *P. petroselinifolium*) could be included in the *Pinnatum* group, and *P. aristatum* fits in well with the *Attenuatum* group.

When all the characters studied are considered, there is no single character that can be used to divide the section in smaller units. Because of the importance of the androecium in the reproductive success of *Hoarea* species, the basis for the subdivision of the section was the variation in the androecium. Secondly, because of the co-evolution between the floral structure and that of the pollen grains in the angiosperms (Hemsley & Ferguson 1985), the structure of the tectum played a major role in constructing this subdivision (Table 5.2). Although the combination androecium-tectum structure seems to give the best results in clustering the species, the composition of several floral groups should be reconsidered (Table 5.2, *Attenuatum*, *Caroli-henrici* and *Punctatum* groups). All other characters studied, support the delimitation of some of the floral groups, but at the same time they can be used as a diagnostic tool in the other groups. The section was subdivided as follows:

1. Stamens shorter than the sepals
 - 1.1 Petals spathulate or ligulate; basic chromosome number $x = 9$ *Fissifolium* group
 - 1.2 Petals spathulate; length/width ratio of posterior petals smaller than five
Pinnatum group
 - 1.3 Petals ligulate; length/width ratio of posterior petals greater than five
Attenuatum group
 - 1.4 Petals small (7--16 x 1--4 mm), wine-red or wine-red blotches, hypanthium short (6--16 mm); tectum of pollen reticulate, with small luminae
Proliferum group

2. Anterior stamens more or less the same length than the sepals
 - 2.1 Petals ligulate, slightly curved, margins undulate; posterior stamen very short, lateral and anterior stamens long
Heterophyllum group
 - 2.2 Posterior and lateral stamens very short, anterior stamens long
Aciculatum group
 - 2.3 Stamens twisted, pollen covered surfaces to the front
Luteum group

3. Stamens long, straight, protrude from the flower
 - 3.1 Differences in the form and size of petals; posterior, lateral and anterior stamens of different lengths
Incrassatum group
 - 3.2 Lateral and anterior petals enclose the stamens
Luteolum group
 - 3.3 Papilionaceous type of flower
Rapaceum group
 - 3.4 Fertile stamens more or less the same length, staminal column papillate
Auratum group

4. Stamens much longer than the sepals
 - 4.1 Fertile stamens more or less the same length, remain straight, staminal column smooth, posterior petals auriculate
Triphyllum group
 - 4.2 Stamens remain straight; scape thick, greenish red, wine-red or reddish brown
Caroli-henrici group
 - 4.3 Stamens curved upwards
Punctatum group

This classification should be regarded as an attempt to bring about a framework for the subdivision of the section which will simplify the study of the unidentified specimens and those species of which the species concept is difficult to define. It should also be considered as a preliminary classification, because some groups seem to be of a heterogeneous constitution (*Caroli-henrici*, *Punctatum* and *Incrassatum* groups). *P. oblongatum* and *P. curviandrum* of the *Punctatum* group have long curved stamens. The androecium of these two species consists of ten filaments of which five are fertile in *P. oblongatum* and four fertile in *P. curviandrum*. The tectum of the pollen of these species is striate-reticulate. *P. triandrum* and *P. punctatum* also have long curved stamens, but with a reduction in the number of filaments and fertile stamens (Tables 7.1 & 7.2). The tectum of both species is extremely striate, and the similarities in the *Punctatum* group

should rather be ascribed to convergent evolution than a phylogenetic relationship. The same kind of differences occur in the *Caroli-henrici* group and to a lesser extent in the *Attenuatum* group, and the similarities could probably be ascribed to convergent development. According to morphological features alone, species with very short stamens should be placed in three different groups: firstly in respect to petal size and pollen structure (*Proliferum* group), and secondly in respect to the length/width ratio of the petals. This second group can be divided in species with ligulate petals (length/width ratio of petals bigger than five) and species with spatulate petals (length/width ratio of petals smaller than five). If chromosome numbers are considered four of these species have the unusual basic chromosome number $x = 9$. If the chromosome numbers and the chromosome sizes of all the other species with short stamens were known, one might come to the conclusion that other characters than petal size and length/width ratio of petals should be used for the subdivision of the section. Chromosome number and chromosome size, as well as DNA studies and chemotaxonomical data could reveal other relationships, additionally to what were revealed by morphological data alone. Cladistic analysis on morphological characters alone proved to be very misleading in *Pelargonium*, as was found in section *Ligularia s.l.* (Van der Walt, personal communication), since convergent evolution seems quite often to be the cause for the development of similar structures in *Ligularia s.l.* As Albers and co-workers are studying the chromosomes at present, and karyological data will be available in the near future, I do not want to regard the floral type groups, mainly based on morphological data, as subsections. With karyological and chemotaxonomical data known, cladistic analysis could be done and subsections should be demarcated with more confidence. Keys for the identification of the species within each subdivision, should then be constructed.

Phylogeny

The evolutionary development of section *Hoarea* follows a radiating pattern and it is very difficult to determine the direction of the evolutionary trends in the section.

The section has a rather limited distribution area when compared with some other sections in the genus. Within this limited distribution area there are several species with a very small distribution, species which are specifically adapted to that special habitat in which annual rainfall probably plays an important isolating role. The majority of species occur in the winter rainfall area. Leaves appear after the first winter rains, and die in summer before or after flowering time. These deciduous-leaved geophytes are dormant during the hot dry summer, an advanced mechanism to survive the unfavourable season (Radford *et al.* 1974).

The stem divisions in *P. appendiculatum* could probably be a transition to the shrub-like *Pelargoniums* or vice versa. *P. appendiculatum* is a tuberous species with a regularly shaped tuber, typical for *Hoarea*, but extensive branching, probably stimulated by grazing of sheep and antelope, resulted in annual stem increments similar to those of *P. stipulaceum* and to a lesser degree to *P. torulosum* E.M. Marais. The latter is a much-branched decumbent shrublet with a succulent, moniliform stem. The older sagging prostrate stems are partly covered by sand, and during winter small globular increments terminated by leaves, appear above ground level. It flowers in November, after which the leaves die and the plants remain dormant until the following winter. During dormancy the stems are covered by sand, probably a way to survive during the hot dry summer (Marais 1990a). This mechanism for survival suggests an evolutionary trend towards geophytism. *P. stipulaceum*, a species closely related to *P. torulosum*, usually occurs between rocks, where the stems are supported by the rocks. *P. stipulaceum* also has sometimes moniliform stems (Marais 1990a), and a very characteristic feature of this species is the large membranous, persistent stipules (Van der Walt & Vorster 1981a), very similar to that of *P. appendiculatum*. Although the survival mechanism of *P. torulosum* indicates an evolutionary trend towards the development of geophytism, which is probably similar to the origin of the geophytes in section *Hoarea*, I regard the stem divisions in *P. appendiculatum* as a secondary development from a geophyte towards a shrublet, because these stem divisions probably develop in reaction to grazing. Plants of *P. appendiculatum*, growing in the protected environment of the garden, develop several stem-growing points typical for section *Hoarea*, and not stem increments as developing in plants exposed to grazing.

Pelargonium flowers are borne in pseudo-umbels with several flowers per inflorescence. The older flowers are borne in the centre and the buds on the periphery. In some sections like *Jenkinsonia* and *Myrrhidium*, there are species with only one or two flowers per inflorescence. In these cases the flowers are borne in the axils of a limited number of bracts (Marais 1981). I regard this as a reduction in the number of flowers in the inflorescence and regard it as a secondary specialization and thus an advanced character. The flowers in these cases are also extremely zygomorphic (Marais 1981). Section *Hoarea* does not show the same evolutionary trend, instead the evolutionary trend point at an increase in the number of flowers. This, according to Radford *et al.* (1974), is generally accepted as the evolutionary trend in flowering plants. According to Rodriguez-Robles *et al.* (1992) the inflorescence size, that is the total number of flowers per inflorescence contributes to the attraction of pollinators, but Wyatt (1982) stressed that the opinion of several experts on this subject is that the aggregation of flowers into a

head is biologically equivalent to a single flower. Burt (1961) pointed out that the latter is true in terms of pollinator attraction, but the advantage of many-flowered inflorescences lies in the much higher outcrossing rates and by that enhancing new gene combinations. By having large numbers of flowers per inflorescences, is probably the mechanism by which *Hoarea* species, which usually occur in small populations, enhance new gene combinations. The majority of species in section *Hoarea* usually have less than fifteen flowers per pseudo-umbellet (Table 3.1). Although not true in the case of *P. ternifolium* and *P. longiflorum*, species with a reduction in the number of fertile stamens tend to have large numbers of flowers per pseudo-umbellet (Table 7.1). The increase in the number of flowers is probably to enhance the male phase in the pollination mechanism (Wyatt 1982). Some species with five fertile stamens (*P. incrassatum*, *P. moniliforme* and *P. rapaceum*) also have large numbers of flowers per pseudo-umbellet.

Table 7.1 Comparison between the reduction in number of fertile stamens and the number of flowers per pseudo-umbellet of some *Hoarea* species.

Species	number of fertile stamens	number of flowers per pseudo-umbellet
<i>P. incrassatum</i>	5	(15-)20--55
<i>P. moniliforme</i>	5	12--40(-50)
<i>P. rapaceum</i>	5	6--30(-47)
<i>P. longiflorum</i>	4, 5	4--15
<i>P. ternifolium</i>	4	3--7
<i>P. githagineum</i>	4	6--27
<i>P. caroli-henrici</i>	4	(10-)15--25(-50)
<i>P. curviandrum</i>	4	7--23(-29)
<i>P. vinaceum</i>	2, 3, 4	(7-)10--27
<i>P. triandrum</i>	3	7--26(-30)
<i>P. confertum</i>	2	13--24(-40)
<i>P. rubiginosum</i>	2	10--30
<i>P. punctatum</i>	2	(10-)17--45(-60)

A similar reduction in the number of fertile stamens occurs in different floral types (Table 7.2) and does not necessarily reveal evolutionary relationships in *Hoarea*. The reduction in the number of fertile stamens can be associated with striate and extremely striate patterns of the tectum (Table 7.2). In plants, both the reduction in floral parts (Radford *et al.* 1974) and the striate pattern of the tectum (Chapter 5) can be regarded as derived characters.

Table 7.2 Floral groups of section *Hoarea* where the reduction of fertile stamens occur with the accompanying tectum structure.

Floral group Species	Number of fertile stamens	Tectum structure
<i>Attenuatum</i> group		
<i>P. longiflorum</i>	4 or 5	reticulate large lumen
<i>Auratum</i> group		
<i>P. ternifolium</i>	4	striate-reticulate
<i>Caroli-henrici</i> group		
<i>P. githagineum</i>	4	striate-reticulate
<i>P. caroli-henrici</i>	4	striate-reticulate
<i>P. rubiginosum</i>	2	extremely striate
<i>Incrassatum</i> group		
<i>P. vinaceum</i>	2, 3, or 4	striate
<i>Punctatum</i> group		
<i>P. curviandrum</i>	4	striate-reticulate
<i>P. triandrum</i>	3	extremely striate
<i>P. punctatum</i>	2	extremely striate
<i>Aciculatum</i> group		
<i>P. confertum</i>	2	striate

Section *Hoarea* with its deciduous geophytes and sometimes extremely zygomorphic flowers, and with its large variation in the floral structure, especially that of the androecium, exhibits advanced morphologic characteristics. These include the striate pattern of the tectum of the pollen grains and the reduction in the number of floral parts (Table 7.3). In comparing section *Hoarea* to the rest of the genus, advanced characters seem to be more numerous in *Hoarea* than in the rest of the genus.

Table 7.3 Reduction in the number of floral parts of section *Hoarea* in comparison with the rest of the genus.

	Section <i>Hoarea</i>	Rest of genus <i>Pelargonium</i>
Petals	5, 4, 2	5, 4, (0)
Stamens	10, 8, 7	10
Fertile stamens	5, 4, 3, 2	7, 6, 5, 4
Carpels	5, 4	5

Previous studies in *Pelargonium* indicated little relationship between the floral structure of section *Hoarea* and the rest of the genus (Marais 1981). From this I deduce that section *Hoarea* parted already at an early stage of the evolutionary history of *Pelargonium* from the rest of the genus. In this process it developed advanced floral structures in which the pollination biology was probably one of the major driving forces in the evolution of the section. At the same time plants developed an advanced growth form as an adaptation to the environment, and rainfall seems to play an important role in the distribution of the different species.

Because of this variation in the androecium a preliminary classification of the section is made. The relative length of the stamens is diagnostic at specific level and varies from much shorter than, the same length as or longer than the calyx. On account of the length of the different stamens and the ratio between the length of the stamens and that of the sepals or the petals, different types of floral structures can be recognized. Other characters in the inflorescence and floral structure were also used in this classification.

The preliminary subdivision is mainly based on external morphology of the plants. Although all morphological characters were considered, the emphasis was on the structure of the androecium. This is because reproduction in any living organism is very important and the development of the androecium and that of the gynoecium are an important safeguard for the survival of any organism. In the species of *Hoarea* like all the species of *Pelargonium*, the gynoecium shows no or little variation. Only the length of the ovary (special that of the rostrum) and the length of the style may differ. Species with long stamens also have long ovaries and styles.