

CHARACTER VARIATION AND A CLADISTIC ANALYSIS OF THE GENUS
Lachenalia Jacq.f. ex Murray (Hyacinthaceae:Massonieae)

by

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Lachenalia bulbifera (Cirillo) Engl. from Pierre-Joseph Redouté's *Les Liliacées*,
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ABSTRACT

Morphological variation and a cladistic analysis of the large, endemic southern African genus *Lachenalia* Jacq.f. ex Murray (Hyacinthaceae: Massonieae) is presented. Its close taxonomic relationship with the small endemic sympatric genus *Polyxena* Kunth (which has been included in the morphological and cladistic study) is discussed. The inclusion of *Polyxena* within *Lachenalia* is supported. One hundred and twenty species (139 taxa), comprising 115 *Lachenalia* and five *Polyxena* species are recognised.

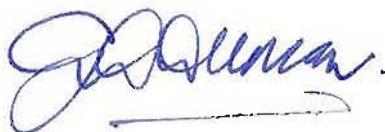
A wide range of morphological characters were analysed, including macromorphology, micromorphology, anatomy and palynology. A discussion and comparison of karyological data is also presented.

A brief historical background, species diversity maps, figures, tables, appendices and illustrations of anatomical, micromorphological and macromorphological characters, and cladistic data, are presented, as well as discussions of pollination biology and phytogeography. This work is based on species studied in their natural habitats as well as under cultivation, and from representative herbarium specimens examined from BOL, NBG, PRE and SAM.

PREFACE

The experimental work described in this dissertation was carried out in the School of Botany and Zoology, University of KwaZulu-Natal, Pietermaritzburg, and at Kirstenbosch National Botanical Garden, Cape Town, from January 1998 to November 2004, under the supervision of Professor Trevor Edwards.

These studies represent original work by the author and have not otherwise been submitted in any form for any degree or diploma to any University. Where use has been made of the work of others it is duly acknowledged in the text.



Signed:

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Signed:

Professor Trevor J. Edwards (supervisor).

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UNPUBLISHED NAME CHANGES IN THIS THESIS

- (a) Combinations awaiting publication used throughout the thesis for expedience.

Lachenalia glauca (W.F.Barker) G.D.Duncan

Lachenalia trichophylla Baker subsp. *massonii* (Baker) G.D.Duncan

- (b) Taxa awaiting publication used throughout the thesis for expedience.

Lachenalia aloides (L.f.) Engl. var. *bonaspei* G.D.Duncan

Lachenalia aloides (L.f.) Engl. var. *piketbergensis* W.F.Barker ex G.D.Duncan

Lachenalia aloides (L.f.) Engl. var. *thunbergii* W.F.Barker ex G.D.Duncan

Lachenalia arida G.D.Duncan

Lachenalia canaliculata G.D.Duncan

Lachenalia contaminata Aiton var. *exserta* G.D.Duncan

Lachenalia cernua G.D.Duncan

Lachenalia fasciculata G.D.Duncan

Lachenalia komsbergensis G.D.Duncan

Lachenalia lutea G.D.Duncan

Lachenalia nardouwensis G.D.Duncan

Lachenalia undulata Masson ex Baker subsp. *grandifolia* G.D.Duncan

Lachenalia urceolata G.D.Duncan

Lachenalia wiesei G.D.Duncan

1 INTRODUCTION

The horticulturally important, and botanically diverse genus *Lachenalia* Jacq.f. ex Murray is endemic to southern Africa, and comprises 115 species in the family Hyacinthaceae. The genus was described by J.A. Murray in 1784, with *L. tricolor* Jacq.f. (now *L. aloides* (L.f.) Engl.) as the type species. *Lachenalia* is morphologically and cytologically variable. *Polyxena* is a paraphyletic genus (Pfosser & Speta 1999, Pfosser *et al.* 2003, van der Merwe 2002, Manning *et al.* 2004) which was established by Kunth in 1843.

The distribution of *Lachenalia* extends from the western and southern parts of Namibia southwards into South Africa, where it occurs in the Richtersveld, western Bushmanland, throughout Namaqualand, the northwestern, western, southwestern and southern parts of the Western Cape, the Great and Little Karoo, and the western, southern, south-eastern and northeastern parts of the Eastern Cape (Duncan 1988a). Its distribution extends as far inland as the central and northeastern parts of the Northern Cape, and the southwestern part of the Free State (Duncan 1996). The genus is geophytic, deciduous, and is usually winter-growing. *Lachenalia* occurs in a wide range of habitats, including arid areas (western and southern Namibia, Richtersveld, western Bushmanland, Namaqualand and northwestern parts of Western Cape), semi-arid areas (Western Cape interior), and medium to high rainfall areas (southwestern and southern parts of Western Cape). The centre of diversity is in the Worcester grid (3319), divided between the Succulent Karoo and Fynbos biomes, in the mountains and valleys of the winter rainfall region in the southwestern part of the Western Cape. Species diversity decreases markedly toward the eastern and northern parts of its range in the Eastern and Northern Cape.

According to Goldblatt & Manning (2000), *Polyxena* comprises five species. A number of investigations (Pfosser & Speta 1999, Pfosser *et al.* 2003, van der Merwe 2002) indicate that it is embedded within *Lachenalia* and therefore it is included within this study. A very recent paper (Manning *et al.* 2004) formalised the synonymisation of *Polyxena* into *Lachenalia*

and the transfer of the species to *Lachenalia*, but appeared too late for incorporation in this thesis. Accordingly in this thesis the species of *Polyxena* are still retained under this genus. *Polyxena* is restricted to the mainly winter rainfall parts of Northern Cape, the western and southern parts of Western Cape, and Eastern Cape. *P. ensifolia* has the widest distribution, extending from southwestern Namaqualand and the western Great Karoo to the southern and southeastern parts of the Eastern and Northern Cape.

Species delimitation in *Lachenalia* is usually unambiguous, but in some instances there is gradation between species. Other species display extensive variation which has led to considerable taxonomic confusion, with overemphasis of minor morphological differences (Duncan 1992). Variation within a species occurs in several macro-morphological characters such as overall plant size, leaf number, pedicel length, degree of stamen exertion, flower size, colour and orientation, and flowering period. Variable species often display population stability in features such as bulb and flower shape, and seed morphology. However, species such as *L. bulbifera*, *L. contaminata*, *L. elegans*, *L. mutabilis*, *L. orchioides*, *L. pustulata* and *L. violacea* are exceedingly variable.

Cytology has shown *Lachenalia* to be unusually variable in chromosome number, sometimes within the same morpho-species, such as in *L. bulbifera*, a polyploid complex, where the basic chromosome number is $x = 7$, but where chromosome number includes $2n = 14, 28, 42, 49$ and 56 (Kleynhans & Spies 1999). Variation in chromosome number creates breeding incompatibility between phenotypically similar individuals. Polyploidy occurs in several other taxa; postulated hypotheses for its presence in *Lachenalia* are discussed in chapter 5.20 under Karyology. Chromosome number of the outgroup *Massonia* includes $2n = 18, 22$ and 26 (Johnson & Brandham 1997), but that of *Polyxena* is unknown. Morphological variation within *Lachenalia* appears to be better correlated to geographical distribution than with ploidy level, as species with similar ploidy levels but with different geographical distribution, differ morphologically (Kleynhans & Spies 1999).

The horticultural potential of *Lachenalia* has been recognised for centuries and many of its species are popular container and bedding subjects throughout the world (Duncan 1988a, Jeppe & Duncan 1989, Du Plessis & Duncan 1989). The high level of morphological variation has made the genus an ideal subject for hybridization (Reid 1985). Hybrid clones can be vegetatively multiplied from peduncles, bulb scales and leaf cuttings (Coertze *et al.* 1992, Duncan 1988a, Perrignon 1992), and by tissue culture (Coertze *et al.* 1992, Nel 1983, Niederwieser & Vcelar 1990). It is only within the past five years that the commercial potential of the genus has begun to be exploited on a large scale, although a breeding programme had already started in 1965 at the erstwhile Horticultural Research Station at Roodeplaat (now the Agricultural Research Council) near Pretoria, with the introduction of selected cultivars onto the world market (Duncan 2001).

The aim of this study was to examine the potential of macromorphological and micromorphological characters in producing a natural classification of *Lachenalia*.

2 HISTORICAL SYNOPSIS

2.1 THE PRE-LINNEAN PERIOD

The first *Lachenalia* species to be recorded was the plant now known as *L. hirta* (Thunb.) Thunb. var. *hirta*, having been depicted in the journal of Simon van der Stel, governor of the Cape of Good Hope, illustrating his expedition to Namaqualand between 1685 & 1686 (Waterhouse 1932, Barker 1988, Wijnands *et al.* 1996). This figure of *L. hirta*, which was later copied and appeared in *Leonardi Plukenetii Phytographia* (1692), was the first illustration of the genus to be published. Subsequently, the most important pre-Linnean publication was the *Flora Capensis of Jacob and Johann Philipp Breyne*, in 1739, in which paintings of three *Lachenalia* species now known as *L. orchioides* (L.) Aiton, *L. orchioides* (L.) Aiton var. *glaucina* (Jacq.) W.F.Barker and *L. contaminata* Aiton appear (Gunn & Du Plessis 1978).

2.2 THE POST-LINNEAN PERIOD

When Linnaeus introduced his binomial classification system (1753), he described the first species as *Hyacinthus orchioides* (now known as *L. orchioides* (L.) Aiton). *Lachenalia* was erected by J.F. Jacquin (1780), in honour of Werner de Lachenal, Professor of Botany and Anatomy at the University of Basel, Switzerland, but it was Murray (1784) who was inadvertently responsible for the publication of the genus in *Systema vegetabilium*. In 1780, Jacquin had sent his manuscript to the editor of *Acta Helvetica*, expecting it to be published that year, but the publication of that journal had lapsed, and Murray, evidently having seen the manuscript and presuming it had been published, included a short description of the genus in *Systema vegetabilium* (Barker 1988). In 1781, Linnaeus *fil.* published *Phormium aloides*, the second *Lachenalia* species of the post-Linnean period, now known as *L. aloides* (L.f.) Engl. In the meantime, plant collections in the Schönbrunn Palace Gardens near Vienna, including many *Lachenalia* species, were increasing rapidly, and being studied by Baron Nikolaus

Joseph von Jacquin and his son Joseph Franz von Jacquin (Garside 1942). N. J. Jacquin published three lavishly illustrated volumes titled *Icones Plantarum Rariorum*, twenty-three colour plates of *Lachenalia* species were included in the first two volumes (Jacquin 1781-1786, 1786-1793), ten of which have become iconotypes due to the destruction of the holotypes during the bombing of Vienna in the Second World War. Several more *Lachenalia* plates appeared in volume one of N.J. Jacquin's (1797) *Plantarum Rariorum Horti Caesari Schönbrunnensis Descriptiones et Icones*. Thunberg (1784) published several taxa under the genus *Phormium*, including *P. hirtum*, the species first illustrated by Simon van der Stel in 1685/6. He later revised his work on the genus under *Lachenalia* (1794), in which *P. hirtum* became *L. hirta* (Thunb.) Thunb.

In the early nineteenth century, Pierre-Joseph Redouté, one of the greatest botanical artists of all time, published his magnificent eight volume work *Les Liliacées* (1802-1816) which included *Lachenalia pendula* (now *L. bulbifera*).

Polyxena was originally described by Kunth (1843) for a species previously placed in *Polyanthes* by N.J. Jacquin (1795), with *P. pygmaea* (Jacq.) Kunth (now *P. ensifolia*) as its sole member, in which both authors cited the biseriate stamens as generically important. Linnaeus (1771) published the first *Polyxena* species, under the name *Hyacinthus corymbosus*, which was subsequently transferred to *Massonia* (Ker Gawler 1807), then to *Scilla* (Ker Gawler 1812), to *Periboea* (Kunth 1843), and finally to *Polyxena corymbosa* (Jessop 1976).

2.3 THE CONTRIBUTION OF J.G. BAKER

Only two monographs of *Lachenalia* have been done, both by Baker. The first appeared in 1871 and included twenty-nine species and an indented key. Several additions were published by various authors in the ensuing twenty-six years before Baker (1897) produced his major and final work on the genus recognizing forty-two species in five subgenera (*Brachyscypha*, *Chloriza*, *Coelanthus*, *Eulachenalia* and *Orchiops*), based on morphological differences.

Most of the species were voucherised with collectors' details and herbarium citations. Some of the diagnostic characters used by Baker (such as leaf number, presence or absence of pustules on leaf surfaces, as well as flower colour and peduncle length) are unreliable. Three of his subgenera (*Brachyscypha*, *Coelanthus* and *Eulachenia*) are distinct in floral morphology but the remaining two are not. Similar-looking species which he included under the same subgenus are not closely related when one examines living material, whereas other dissimilar-looking species which were placed in different subgenera have proved to be related and interfertile (Hancke & Liebenberg 1998). Baker (1897) recognised four species in his concept of *Polyxena* subgenus *Eupolyxena*, as well as two species of *Hyacinthus* from the southwestern Cape, but Jessop (1976) treated most species in this subgenus as synonymous (as *P. ensifolia*), and combined the two Cape species of *Hyacinthus* under *Polyxena* as *P. corymbosa*.

During the latter part of the nineteenth century, many more *Lachenalia* species were discovered by various collectors, the most prominent collector being the German botanist and traveller Rudolph Schlechter, who was active between 1891-1898 (Gunn & Codd 1981). He deposited undescribed duplicate material in 15 herbaria in Europe, Scandinavia and South Africa. Some of these he had given manuscript names to, while others were not identified at specific level. Jessop (1964) published an itinerary of Schlechter's collecting trips in southern Africa, and Barker (1983a) published a list of Schlechter's *Lachenalia* collections, with identifications.

2.4 THE CONTRIBUTION OF W.F. BARKER

Most of the subsequent taxonomic work on *Lachenalia* was done by Barker, first Curator of the Compton Herbarium (Duncan 1998b). She published forty-seven new species and eleven new varieties for the genus, including many collected by Rudolph Schlechter (Barker 1930a, b, 1931a, b, c, 1933a, b, c, d, 1949, 1950, 1966, 1969, 1972, 1978, 1979a, b, 1980, 1983b, 1984, 1987, 1988, 1989). She also published *Polyxena maughanii* from the western

Karoo (Barker 1931d), and *Hyacinthus paucifolius* (now *P. paucifolia*), a narrow endemic of the Cape west coast (Barker 1941). Over a period of forty-three years (1929-1972) she undertook extensive collecting trips and assembled the most comprehensive collection of herbarium specimens of *Lachenalia* in the world. She illustrated many new species with line drawings or watercolour paintings, which often accompanied her taxonomic papers. She continued her taxonomic work after her retirement in 1972, and her final contribution (Barker 1989) dealt with two new species and six new varieties of *Lachenalia*, as well as several nomenclatural changes for the genus. One of Barker's greatest contributions to the knowledge of the genus was the use of seed morphology as a useful diagnostic character in delimiting many species (Barker 1978, 1979a, 1983b, 1984, 1987, 1989).

2.5 RECENT DEVELOPMENTS

Crosby (1986) published a lengthy paper in 'The Plantsman' titled 'The genus *Lachenalia*', in which a subgeneric classification system was proposed based on chromosome studies and hybridisation experiments of thirty-four cultivated species, placed in five groups, with each group based on a species type, namely the 'L. aloides', 'L. orchioides', 'L. pusilla', 'L. unicolor' and 'L. unifolia' groups. A historical review by Crosby (1978) of hybridisation in the genus was also presented.

Duncan (1988a) provided an illustrated identification guide to the eighty-eight *Lachenalia* species recognised at that time, and divided the genus into two major groups (based on stamen length in relation to the tip of the perianth segments), and ten subgroups (based on inflorescence types). This study was based on the living collection at Kirstenbosch Botanic Garden at the National Botanical Institute, and the comprehensive herbarium specimen collection at the Compton Herbarium at the same institution, as well as field research.

Johnson & Brandham (1997) published an extensive list of chromosome numbers for *Lachenalia*, and recorded new basic chromosome numbers of $x = 5, 10$ and 15 . Dold &

Phillipson (1998) produced a revision of the eight *Lachenalia* species occurring in the Eastern Cape. Recent cytological studies in *Lachenalia* by Spies *et al.* (2000, 2002) have contributed to the knowledge of several variable, widely distributed species. Since 1993, sixteen new species and one new subspecies have been published (Duncan 1993, 1996, 1997, 1998a, Duncan & Edwards 2002), and two old species, *L. bowieana* Baker and *L. latifolia* Trattinnick have been reduced to synonymy under *L. nervosa* Ker Gawl. (Duncan & Linder Smith 1999b). A fifth *Polyxena* species, *P. longituba*, a narrow endemic of the Komsberg in the Northern Cape, was published by van der Merwe & Marais (2001). A very recent paper formalised the synonomisation of *Polyxena* into *Lachenalia* and the transfer of five species to *Lachenalia* (Manning *et al.* 2004).

3 MATERIALS AND METHODS

This study was based on wild collections and the extensive, cultivated collection at Kirstenbosch National Botanical Garden in Cape Town, as well as the comprehensive collection of herbarium specimens housed in the Compton Herbarium (NBG). A total of 120 species (139 taxa) were studied. *Massonia depressa* was used as the outgroup. Voucher specimens are lodged at the Compton Herbarium (NBG). Data on the distribution of *Lachenalia* and *Polyxena* were compiled from herbarium material at NBG, the South African Museum (SAM), Bolus Herbarium (BOL) and the National Herbarium, Pretoria (PRE). Photographic records were taken with a Pentax P30N single-lens reflex camera equipped with a 50 mm macro lens. Detailed materials and methods employed in this thesis have been subdivided and placed at the beginning of the relevant chapters. Cladistic data are placed under Phylogeny in Chapter 10.

4 GENERIC DELIMITATION

Since Baker's 1897 revision, the most important reviews of the genera of the Liliaceae *sensu lato* were provided by Krause (1930), Phillips (1951), Hutchinson (1959) and Jessop (1975). Krause (1930), considered most genera to belong to a single major tribe which he called the Scilloideae, including *Lachenalia* and *Polyxena*, whereas Phillips (1951) recognised almost all previously described genera, including *Lachenalia*, and linked *Massonia* with *Polyxena*, but made no attempt at revising tribal groupings of previous researchers. Hutchinson (1959) recognised *Lachenalia* and *Polyxena* as part of tribe Scilleae, and also recognised tribes Massonieae and Bowieae. Jessop (1975) used microsculpturing of seed surfaces of 25 genera of South African Liliaceae *sensu lato* to support three tribes, namely Scilleae, Bowieae and Massonieae. *Lachenalia* and *Polyxena* were placed in the Massonieae.

As a result of the widely accepted restructuring of the Liliaceae *sensu lato* by Dahlgren & Clifford (1982), and Dahlgren *et al.* (1985), as well as the recent phylogenetic analysis of plastid DNA sequence data of Pfosser & Speta (1999), Pfosser *et al.* (2003), and seed morphological studies of Wetschnig *et al.* (2002), the classification of *Lachenalia* and *Polyxena* used in this thesis is as follows:

Superorder	LILIIFLORAE
Order	Asparagales
Family	Hyacinthaceae
Subfamily	Hyacinthoideae
Tribe	Massonieae
Genus	<i>Lachenalia</i>

Species and Year of publication, arranged chronologically

<i>L. orchioides</i> (L.) Aiton (two taxa).....	(1753)
<i>L. aloides</i> (L.f.) Engl. (eight taxa).....	(1781)
<i>L. hirta</i> (Thunb.) Thunb. (two taxa).....	(1784)
<i>L. bulbifera</i> (Cirillo) Engl.	(1788)
<i>L. contaminata</i> Aiton (two taxa).....	(1789)
<i>L. mediana</i> Jacq. (two taxa).....	(1789)
<i>L. orthopetala</i> Jacq.	(1789)
<i>L. pustulata</i> Jacq.	(1789)
<i>L. violacea</i> Jacq.	(1790)
<i>L. patula</i> Jacq.	(1790)
<i>L. reflexa</i> Thunb.	(1794)
<i>L. rubida</i> Jacq.	(1794)
<i>L. isopetala</i> Jacq.	(1794)
<i>L. liliiflora</i> Jacq.	(1794)
<i>L. purpureocaerulea</i> Jacq.	(1794)
<i>L. pusilla</i> Jacq.	(1795)
<i>L. unicolor</i> Jacq.	(1795)
<i>L. unifolia</i> Jacq. (two taxa).....	(1797)
<i>L. rosea</i> Andrews	(1803)
<i>L. nervosa</i> Ker Gawl.	(1812)

Species and Year of publication, arranged chronologically

<i>L. mutabilis</i> Sweet	(1825)
<i>L. anguinea</i> Sweet	(1826)
<i>L. juncifolia</i> Baker (two taxa)	(1871)
<i>L. carnosa</i> Baker	(1871)
<i>L. convallarioides</i> Baker	(1871)
<i>L. campanulata</i> Baker	(1874)
<i>L. trichophylla</i> Baker (two taxa)	(1874)
<i>L. zeyheri</i> Baker	(1874)
<i>L. fistulosa</i> Baker	(1884)
<i>L. undulata</i> Masson ex Baker (two taxa)	(1886)
<i>L. bachmannii</i> Baker	(1892)
<i>L. polyphylla</i> Baker	(1892)
<i>L. bowkeri</i> Baker	(1897)
<i>L. youngii</i> Baker	(1897)
<i>L. dasybotrya</i> Diels	(1909)
<i>L. splendida</i> Diels	(1909)
<i>L. algoensis</i> Schönland	(1910)
<i>L. pearsonii</i> (P.E.Glover) W.F.Barker	(1915)
<i>L. klinghardtiana</i> Dinter	(1929)
<i>L. buchbergensis</i> Dinter	(1929)
<i>L. comptonii</i> W.F.Barker	(1930)
<i>L. muirii</i> W.F.Barker	(1930)
<i>L. longibracteata</i> E.Phillips	(1931)
<i>L. mathewsii</i> W.F.Barker	(1931)
<i>L. haarlemensis</i> Fourc.	(1932)
<i>L. elegans</i> W.F.Barker (four taxa)	(1933)
<i>L. gillettii</i> W.F.Barker	(1933)
<i>L. salteri</i> W.F.Barker	(1933)

Species and Year of publication, arranged chronologically

<i>L. capensis</i> W.F.Barker	(1949)
<i>L. variegata</i> W.F.Barker	(1949)
<i>L. framesii</i> W.F.Barker	(1966)
<i>L. viridiflora</i> W.F.Barker	(1972)
<i>L. concordiana</i> Schltr. ex W.F.Barker	(1978)
<i>L. congesta</i> W.F.Barker	(1978)
<i>L. esterhuysenae</i> W.F.Barker	(1978)
<i>L. glaucophylla</i> W.F.Barker	(1978)
<i>L. montana</i> Schltr. ex W.F.Barker	(1978)
<i>L. multifolia</i> W.F.Barker	(1978)
<i>L. namaquensis</i> Schltr. ex W.F.Barker	(1978)
<i>L. peersii</i> Marloth ex W.F.Barker	(1978)
<i>L. sargeantii</i> W.F.Barker	(1978)
<i>L. verticillata</i> W.F.Barker	(1978)
<i>L. bolusii</i> W.F.Barker	(1979)
<i>L. latimerae</i> W.F.Barker	(1979)
<i>L. macgregorium</i> W.F.Barker	(1979)
<i>L. margaretae</i> W.F.Barker	(1979)
<i>L. marginata</i> W.F.Barker (two taxa).....	(1979)
<i>L. martinae</i> W.F.Barker	(1979)
<i>L. maximiliani</i> Schltr. ex W.F.Barker	(1979)
<i>L. polypodantha</i> Schltr. ex W.F.Barker	(1979)
<i>L. stayneri</i> W.F.Barker	(1979)
<i>L. ventricosa</i> W.F.Barker	(1979)
<i>L. ameliae</i> W.F.Barker	(1983)
<i>L. giessii</i> W.F.Barker	(1983)
<i>L. moniliformis</i> W.F.Barker	(1983)
<i>L. nordenstamii</i> W.F.Barker	(1983)

Species and Year of publication, arranged chronologically

<i>L. whitehillensis</i> W.F.Barker	(1983)
<i>L. zebrina</i> W.F.Barker	(1983)
<i>L. arbuthnotiae</i> W.F.Barker	(1984)
<i>L. physocaulos</i> W.F.Barker	(1984)
<i>L. schelpei</i> W.F.Barker	(1984)
<i>L. barkeriana</i> U.Müll.-Doblies <i>et al.</i>	(1987)
<i>L. dehoopensis</i> W.F.Barker	(1987)
<i>L. kliprandensis</i> W.F.Barker	(1987)
<i>L. leomontana</i> W.F.Barker	(1987)
<i>L. minima</i> W.F.Barker	(1987)
<i>L. namibiensis</i> W.F.Barker	(1987)
<i>L. angelica</i> W.F.Barker	(1989)
<i>L. duncanii</i> W.F.Barker	(1989)
<i>L. thomasiae</i> W.F.Barker ex G.D.Duncan	(1993)
<i>L. alba</i> W.F.Barker ex G.D.Duncan	(1996)
<i>L. karooica</i> W.F.Barker ex G.D.Duncan	(1996)
<i>L. neilii</i> W.F.Barker ex G.D.Duncan	(1996)
<i>L. perryae</i> G.D.Duncan	(1996)
<i>L. aurioliae</i> G.D.Duncan	(1997)
<i>L. inconspicua</i> G.D.Duncan	(1997)
<i>L. marlothii</i> W.F.Barker ex G.D.Duncan	(1997)
<i>L. obscura</i> Schltr. ex G.D.Duncan	(1997)
<i>L. xerophila</i> Schltr. ex G.D.Duncan	(1997)
<i>L. attenuata</i> W.F.Barker ex G.D.Duncan	(1998)
<i>L. doleritica</i> G.D.Duncan	(1998)
<i>L. lactosa</i> G.D.Duncan	(1998)
<i>L. leipoldtii</i> G.D.Duncan	(1998)
<i>L. nutans</i> G.D.Duncan	(1998)

Species and Year of publication, arranged chronologically

<i>L. valeriae</i> G.D.Duncan	(2002)
<i>L. arida</i> G.D.Duncan	(unpublished)
<i>L. canaliculata</i> G.D.Duncan	(unpublished)
<i>L. cernua</i> G.D.Duncan	(unpublished)
<i>L. fasciculata</i> G.D.Duncan	(unpublished)
<i>L. glauca</i> (W.F.Barker) G.D.Duncan	(unpublished)
<i>L. komsbergensis</i> G.D.Duncan	(unpublished)
<i>L. lutea</i> G.D.Duncan	(unpublished)
<i>L. nardouwensis</i> W.F.Barker ex G.D.Duncan	(unpublished)
<i>L. urceolata</i> G.D.Duncan	(unpublished)
<i>L. wiesei</i> G.D.Duncan	(unpublished)

Genus *Polyxena*

<i>P. corymbosa</i> (L.) Jessop	(1771)
<i>P. ensifolia</i> (Thunb.) Schönland	(1794)
<i>P. maughanii</i> W.F.Barker	(1931)
<i>P. paucifolia</i> (W.F.Barker) A.M.van der Merwe & J.C.Manning	(1941)
<i>P. longituba</i> A.M.van der Merwe	(2001)

Following the very recent synonymisation of *Polyxena* into *Lachenalia*, and the transfer of the species to *Lachenalia* (Manning *et al.* 2004), the new combinations accepted by the author, are as follows:

Genus	<i>Lachenalia</i>
	<i>L. corymbosa</i> (L.) J.C.Manning & Goldblatt
	<i>L. ensifolia</i> (Thunb.) J.C.Manning & Goldblatt
	<i>L. maughanii</i> (W.F.Barker) J.C.Manning & Goldblatt
	<i>L. paucifolia</i> (W.F.Barker) J.C.Manning & Goldblatt
	<i>L. longituba</i> (A.M.van der Merwe) J.C.Manning & Goldblatt

The subcosmopolitan family Hyacinthaceae comprises approximately 900 species worldwide, with the greatest diversity in South Africa and the Mediterranean (Speta 1998a). The family comprises four subfamilies Hyacinthoideae, Ornithogaloideae, Oziroeoideae and Urgineoideae, based on molecular, morphological, karyological and chemotaxonomic data (Pfosser & Speta 1999, 2001). The subfamily Hyacinthoideae is further divided into tribes comprising the Northern Hemisphere tribe Hyacintheae, the mainly Southern Hemisphere tribe Massonieae, and the endemic, monotypic South African tribe Pseudoprosperae (Manning *et al.* 2004). With the exception of *Pseudoprospero*, all southern African genera in the Hyacinthoideae cluster together within the tribe Massonieae. Currently the tribe Massonieae includes 10 genera comprising *Daubenya*, *Eucomis*, *Lachenalia* (including *Polyxena*), *Ledebouria*, *Massonia*, *Merwillia*, *Namophila*, *Schizocarphus*, *Spetaea* and *Veltheimia* (Manning *et al.* 2004).

The generic delimitation of the dwarf species *Lachenalia pusilla* has been problematic since its original publication (Jacquin 1795). It was regarded as a monotypic genus *Brachyscypha* by Baker (1871), which was reincorporated into *Lachenalia* by Bentham and Hooker (1883) as section *Brachyscypha*. Baker accepted the latter placement in his subsequent revision of the genus (1897), but Schlechter (1924) incorrectly transferred it to *Polyxena* due to its biseriate stamens, apparently unaware that this character occurs in all *Lachenalia* species. Müller-Doblies *et al.* (1987) confirmed Baker's (*l.c.*) placement of *L. pusilla* in subgenus *Brachyscypha*, and described *L. barkeriana*, a closely related species belonging to this subgenus. However, they erroneously considered *Polyxena* distinct from *Lachenalia* on the

grounds of three macro-morphological characters:

1. Floral symmetry - actinomorphic flowers for *Polyxena* as opposed to at least very slightly zygomorphic flowers for *Lachenalia*. One *Lachenalia* species (*L. pearsonii*) has actinomorphic flowers.
2. Perianth tube length - longer than half the length of the perianth in *Polyxena*, versus less than one quarter the length of the perianth in *Lachenalia*. Two *Lachenalia* species (*L. reflexa* and *L. viridiflora*) have perianth tubes longer than half the length of the perianth.
3. Inner tepal length - equal to or shorter than the outer tepals in *Polyxena*, versus nearly always longer than the outer ones in *Lachenalia*. Numerous *Lachenalia* species have subequal tepals (e.g. *L. buchbergensis*, *L. campanulata*, *L. isopetala*).

The work of Müller-Doblies & Müller-Doblies (1997) also contradicts recent molecular research (Pfosser & Speta 1999, Pfosser *et al.* 2003, van der Merwe 2002, Manning *et al.* 2004) which indicates a paraphyletic relationship between *Lachenalia* and *Polyxena*. Müller-Doblies & Müller-Doblies (1997) placed these two genera in two different subtribes of the Massonieae. They placed *Lachenalia* in subtribe Lachenaliinae, based on “the perianth arising obliquely from the pedicel, and the insertion of the stamens forming an oblique ring in the perianth tube”. The perianth of almost all *Lachenalia* species is oblique to the pedicel, but this is not the case in the actinomorphic, widely campanulate flowers of *L. pearsonii*. The insertion of the stamens in most *Lachenalia* species is distinctly biseriate and cannot accurately be described as “forming an oblique ring”. Müller-Doblies & Müller-Doblies (1997) placed *Polyxena* in subtribe Massoniinae, based on “the perianth arising radially from the pedicel, and the insertion of the stamens at the throat of the perianth tube”. The perianths of *Polyxena* species do arise radially from the pedicel, but the insertions of the stamens of three species (*P. corymbosa*, *P. maughanii* and *P. paucifolia*) are not confined to the throat of the perianth tube, and are also inserted well within the perianth tube.

With the inclusion of *Polyxena* (*sensu* Pfosser & Speta 1999, Pfosser *et al.* 2003, van der Merwe 2002, Manning *et al.* 2004), *Lachenalia* becomes a well defined genus which is easily distinguished from other genera in the Hyacinthaceae by floral, vegetative and seed characters.

5 MORPHOLOGY

Morphological characters are features of external form or appearance and currently provide most of the characters used for practical plant identification, and many of those used for hypothesizing phylogenetic relationships. These features have been used for a longer time than anatomic or molecular data and have constituted the primary source of taxonomic evidence since the beginnings of plant systematics (Judd *et al.* 1999). Phylogenetically informative characters may be found in both vegetative parts (e.g. bulbs, cataphylls and leaves) and reproductive parts (e.g. flowers, fruits and seeds) of *Lachenalia*. Morphological characters can be of two kinds, either discrete (qualitative) characters in which two or more discrete character states occur, or continuous (quantitative) characters, in which continuous variables occur, such as in length of plant parts where overlapping occurs between species (Scotland 1992).

5.1 MATERIALS AND METHODS

Character data were obtained from as wide a range of variation within species as possible. Qualitative characters such as bulb and seed shape were used where these formed clear evolutionary states. Quantitative characters such as tepal length and filament angles of divergence were used only where dimensional data formed clear, discontinuous units, and plotted onto box and whisker graphs to substantiate the recognition of these as character states. A minimum of 25 samples were measured for each taxon where sufficient material was available. The box and whisker plots convey the following information:

Lower quartile = Bottom line of the box

Median = Middle line of the box

Upper quartile = Top line of the box

Lower whisker = Lower adjacent value. This is equal to the maximum of (i) lower quartile

minus 1.5 times the inter-quartile range and (ii) the minimum observation.

Upper whisker = Upper adjacent value. This is equal to the minimum of (i) upper quartile plus 1.5 times the inter-quartile range and (ii) the maximum observation.

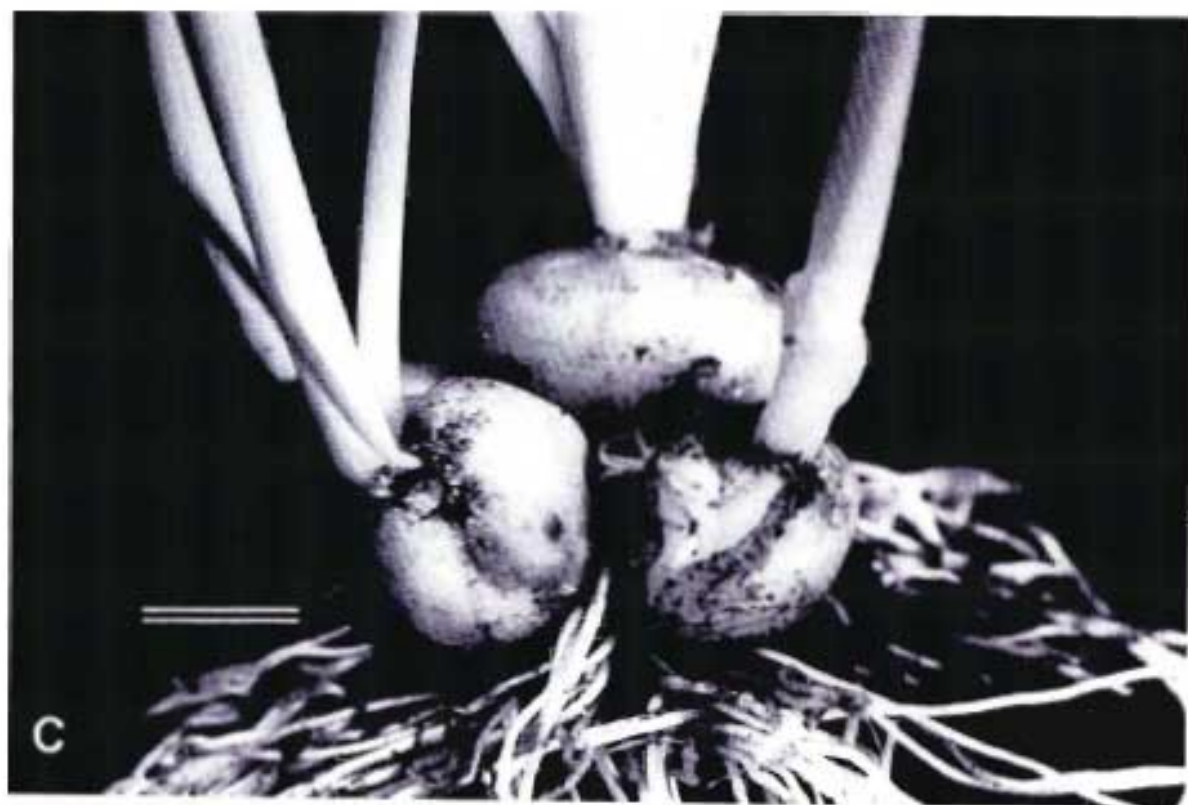
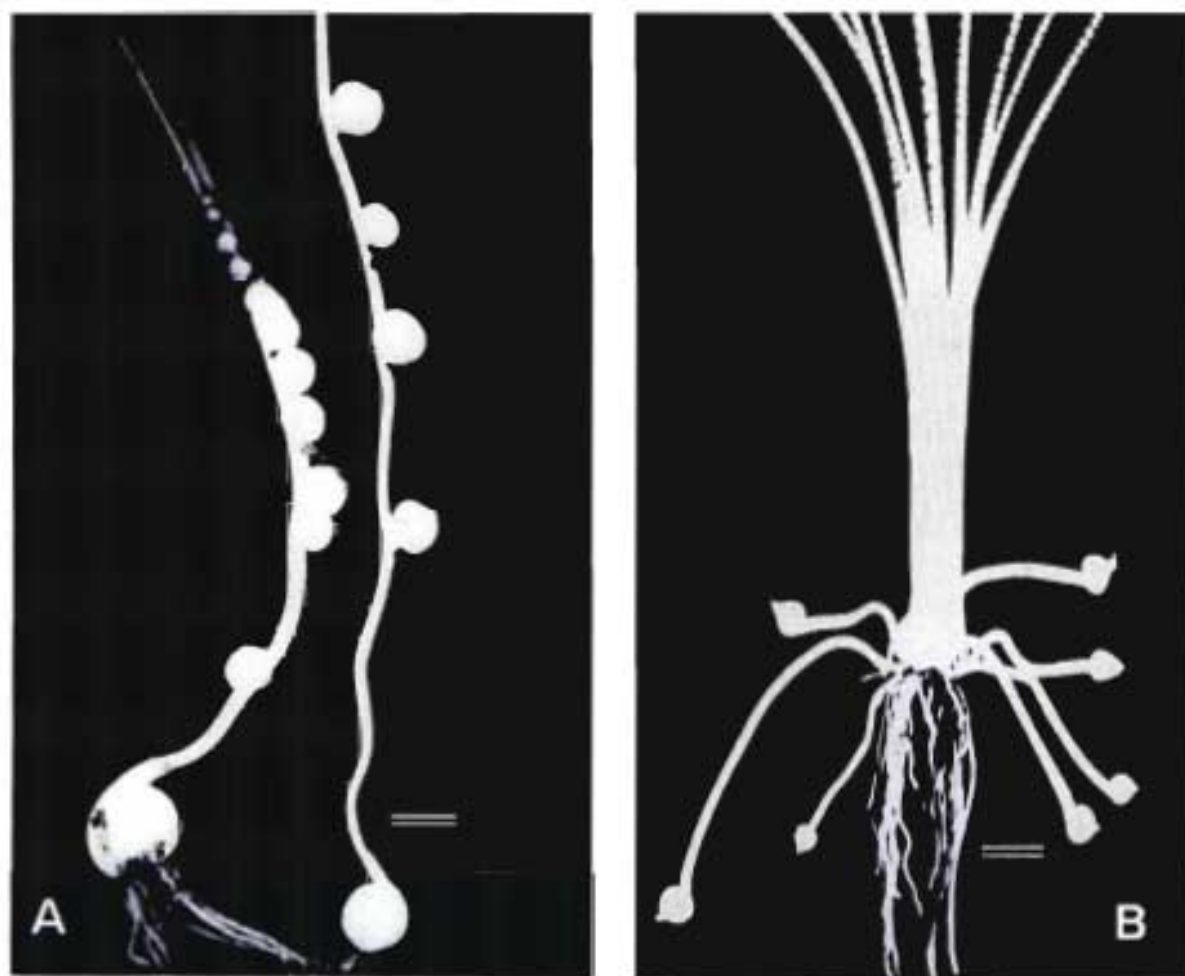
Box width = The variable box width conveys information about the size of the sample.

The cladistic score for each character state is provided in the results for each character.

5.2 HABIT

Lachenalia, *Polyxena* and the outgroup *Massonia* are bulbous, deciduous geophytes (Du Plessis & Duncan 1989). Only one *Lachenalia* species from the summer rainfall area (*L. pearsonii* from inland southern Namibia) has a summer-growing cycle. All other *Lachenalia* and *Polyxena* species growing in the winter rainfall or summer rainfall areas have winter growing cycles (Duncan & Anderson 1999). Plant size in the two genera varies from 5 mm high with a rosette of leaves appressed to the ground and a subcapitate inflorescence produced at ground level (*L. pusilla*), to 600 mm tall (*L. anguinea*) with a many-flowered, racemose inflorescence produced on a robust, inflated peduncle and a single long, canaliculate, flaccid leaf.

L. bulbifera frequently produces bulbils on the subterranean and aerial margins of its clasping leaf bases (Figure 1 A).



Character State	Species
Bulbs solitary	<i>L. ameliae</i> , <i>L. angelica</i> , <i>L. arida</i> , <i>L. attenuata</i> , <i>L. barkeriana</i> , <i>L. buchbergensis</i> , <i>L. carnosae</i> , <i>L. comptonii</i> , <i>L. concordiana</i> , <i>L. congesta</i> , <i>L. dasybotrya</i> , <i>L. doleritica</i> , <i>L. duncanii</i> , <i>L. fasciculata</i> , <i>L. giessii</i> , <i>L. glaucophylla</i> , <i>L. inconspicua</i> , <i>L. isopetala</i> , <i>L. karooica</i> , <i>L. kliprandensis</i> , <i>L. komsbergensis</i> , <i>L. leipoldtii</i> , <i>L. marlothii</i> , <i>L. martinae</i> , <i>L. nervosa</i> , <i>L. nordenstamii</i> , <i>L. nutans</i> , <i>L. pearsonii</i> , <i>L. physocaulos</i> , <i>L. polypodantha</i> , <i>L. pusilla</i> , <i>L. salteri</i> , <i>L. stayneri</i> , <i>L. trichophylla</i> (both subspecies), <i>L. undulata</i> (both subspecies), <i>L. valeriae</i> , <i>L. ventricosa</i> , <i>L. verticillata</i> , <i>L. whitehillensis</i> , <i>L. xerophila</i> , <i>L. zebra</i> <i>Massonia</i>
Bulbs offset-forming	<i>L. alba</i> , <i>L. algoensis</i> , <i>L. aloides</i> (all eight varieties), <i>L. anguinea</i> , <i>L. arbutnotiae</i> , <i>L. aurioliae</i> , <i>L. bachmannii</i> , <i>L. bolusii</i> , <i>L. bowkeri</i> , <i>L. bulbifera</i> , <i>L. campanulata</i> , <i>L. canaliculata</i> , <i>L. capensis</i> , <i>L. cernua</i> , <i>L. contaminata</i> (both varieties), <i>L. convallarioides</i> , <i>L. dehoopensis</i> , <i>L. elegans</i> (all four varieties), <i>L. esterhuysenae</i> , <i>L. fistulosa</i> , <i>L. framesii</i> , <i>L. gillettii</i> , <i>L. glauca</i> , <i>L. haarlemensis</i> , <i>L. hirta</i> (both varieties), <i>L. juncifolia</i> (both varieties), <i>L. klinghardtiana</i> , <i>L. lactosa</i> , <i>L. latimerae</i> , <i>L. leomontana</i> , <i>L. liliiflora</i> , <i>L. longibracteata</i> , <i>L. lutea</i> , <i>L. macgregoriorum</i> , <i>L. margaretae</i> , <i>L. marginata</i> (both subspecies), <i>L. mathewsii</i> , <i>L. maximiliani</i> , <i>L. mediana</i> (both varieties), <i>L. minima</i> , <i>L. moniliformis</i> , <i>L. montana</i> , <i>L. muirii</i> , <i>L. multifolia</i> , <i>L. mutabilis</i> , <i>L. namaquensis</i> , <i>L. namibiensis</i> , <i>L. nardouwensis</i> , <i>L. neilii</i> , <i>L. obscura</i> , <i>L. orchioides</i> (both varieties), <i>L. orthopetala</i> , <i>L. patula</i> , <i>L. peersii</i> , <i>L. perryae</i> , <i>L. polyphylla</i> , <i>L. purpureocaerulea</i> , <i>L. pustulata</i> , <i>L. reflexa</i> , <i>L. rosea</i> , <i>L. rubida</i> , <i>L. sargeantii</i> , <i>L. schelpei</i> , <i>L. splendida</i> , <i>L. thomasiae</i> , <i>L. unicolor</i> , <i>L. unifolia</i> (both varieties), <i>L. urceolata</i> , <i>L. variegata</i> , <i>L. violacea</i> , <i>L. viridiflora</i> , <i>L. wiesei</i> , <i>L. youngii</i> , <i>L. zeyheri</i> <i>P. corymbosa</i> , <i>P. ensifolia</i> , <i>P. longituba</i> , <i>P. maughanii</i> , <i>P. paucifolia</i>

Offsets and bulbils begin to form towards the end of the winter-growing period, from early to late spring, and undergo dormancy in the same way that mature bulbs do from early summer to early autumn. Towards the end of the growing season, several species such as *L. neilii*, *L. montana* and *L. sargeantii* produce bulblets on very short, erect, stalk-like structures up to 4 mm long, arising from the base of the bulb. These bulblets originate in the axils of scales (Roodbol & Niederwieser 1998).

The arid habitats where many *Lachenalia* species occur such as the Richtersveld, Namaqualand, Bushmanland and Knersvlakte, are frequently subject to prolonged drought and erratic rainfall patterns during the normal winter growing period, but the bulbs of species in these areas are adapted to remain dormant for many years, until favourable conditions return (Duncan 2003b).

In cultivation, the bulbs of a number of *Lachenalia* species notably *L. martinae*, *L. nervosa*, *L. peersii*, *L. polypodantha* and *L. zebrina*, periodically remain completely dormant during the normal winter growing-season, for one or more consecutive growing seasons (Duncan & Linder Smith 1999b, Duncan & Visagie 2001). This sporadic phenomenon, which does not occur in the outgroup *Massonia* or in *Polyxena*, has been noted over many years in the collection at Kirstenbosch Botanic Garden, while other bulbs from the same collection continue to grow normally.

5.2.1 Results

Two vegetative characters were defined for the cladistic analyses:

1) **Bulbil production.** Two states occurred: non-soboliferous (=0) and soboliferous (=1) species. Qualitative character, scored as character 3 (Appendix 1).

Non-soboliferous bulbs occurred in *Massonia* and 117 (97.5%) ingroup species (112 *Lachenalia*, all five *Polyxena*). The bulbs of three (2.5%) *Lachenalia* species (*L. bulbifera*, *L. moniliformis* and *L. namaquensis*) were soboliferous, and increased in numbers by the formation of bulbils produced at the tips of horizontal, subterranean stolons up to 150 mm long, resulting in large colonies (Figure 1 B).

2) **Offset production.** Two states occurred: solitary bulbs that never reproduced vegetatively (=0), and offset-forming bulbs (=1). Qualitative character, scored as character 4 (Appendix 1).

Solitary bulbs occurred in *Massonia* and 41 (34%) *Lachenalia* species. In 79 (66%) ingroup species (74 *Lachenalia*, all five *Polyxena*) the bulbs reproduced vegetatively by the formation of offsets (daughter bulbs) (Figure 1 C, Table 1).

Several *Lachenalia* species produced numerous offsets in a ring around the base of the bulb, as in *L. contaminata*, *L. orthopetala* and *L. viridiflora*, but most produced only one or two offsets per growing season, such as in *L. multifolia* and *P. corymbosa*. Offsets formed mainly in the axils of the oldest leaf bases but also occurred in the axils of the younger leaf bases.

5.3 ROOTS

5.3.1 Results

Two types of adventitious roots were produced from the bulbs of all *Lachenalia* and *Polyxena* species, namely fibrous (non-contractile) roots, and thicker contractile roots, both were annual and desiccated completely during the hot dry dormant period (Figure 2).



Figure 2. Variation in root types in *Lachenalia*. a = fibrous root; b = contractile root of *L. rubida* (Duncan 442).

Scale bar = 10 mm.

Root primordia began to develop on dormant bulbs around the periphery of the basal plate as soon as night temperatures began to drop, towards the end of summer, from mid- to late February in the Southern Hemisphere, and were followed by the production of leaf shoots in early autumn. Fibrous roots were produced in abundance in all species. They were brittle, branched or unbranched, with a diameter ranging from 0.5-1.0 mm, and a length of up to 45 mm. Contractile roots were strongly developed in the species which had relatively deep-seated bulbs which were stimulated to flower by natural veld fires (*L. montana*, *L. sargeantii*), as well as certain species which occurred in deep littoral sand dunes (*L. bulbifera*, *L. rubida*). The contractile roots of *L. montana* and *L. sargeantii* pulled the bulbs deeply into the soil, ensuring that they were not damaged by excessive heat during veld fires. Contractile roots were harder and thicker than fibrous roots and, following contraction, had transverse wrinkles and were also generally longer (up to 60 mm), with diameters from 1.5 to 2.5 mm. Roots did not form qualitative or clearly discontinuous quantitative characters in *Lachenalia* and were not included in the character list.

5.4 BULB

A bulb is a specialised subterranean (or partly subterranean) organ that consists of a very short, compressed, conically shaped stem (the basal plate) which is vertically orientated and has a regenerative bud or growing point, the centrally situated apex, often referred to as the apical meristem (Du Plessis & Duncan 1989). The storage and perennating organ in *Lachenalia* and *Polyxena* is a well developed, hypogeal bulb (Duncan 1988a). The bulbs of most geophytes are constructed by a series of morphologically equal, consecutive units or modules (Bell 1991). In *Lachenalia* and *Polyxena*, the development of the bulb is sympodial, as it is constructed by a series of two (inner and outer) consecutive units or modules attached to a dome-shaped, compressed stem, the basal plate. The new (inner) module is situated inside the old (outer) module (Du Toit *et al.* 2001). At the beginning of the growing period, the old module consists of a dry, papery or cartilaginous tunic (formed from the second cataphyll in the previous growth cycle) and, depending on the species, one, two or more

thickened leaf bases from the discarded leaf laminae of the previous growth cycle. The new module usually comprises two cataphylls, and two or more scale leaves, which enclose the leaf primordia and the inflorescence. The first (outermost) cataphyll of the outer module disintegrates at the end of the flowering period (Roodbol & Niederwieser 1998).

5.4.1 Results

Bulb size was extremely variable in *Lachenalia*. The species with the smallest bulb was *L. patula*, whose adult bulb reached a diameter of only 8-9 mm, whereas *L. bulbifera* and *L. rubida* had the largest bulbs, with a diameter of up to 35 mm. The bulbs of the outgroup *Massonia* and most *Lachenalia* and *Polyxena* species fell between 15 and 20 mm in diameter. Bulb size did not form clearly discontinuous classes in *Lachenalia* and *Polyxena* and was not used in the cladistic analyses.

Bulb depth was highly variable in *Lachenalia*. Species which occur in deep white or red sand on litoral or inland dunes such as *L. rubida* and *L. anguinea*, respectively, had bulbs buried up to 170 mm deep. Similarly, the two species which are stimulated into flowering only by the effect of natural veld fires (*L. montana* and *L. sargeantii*), and occur in montane habitats in deep acid sandstone, had bulbs buried up to 100 mm deep. However, the bulbs of most *Lachenalia* and *Polyxena* species rested between 5-15 mm below the soil surface. This was often associated with substrate conditions such as shallow depressions of granite rock sheets (*L. pustulata*, *P. paucifolia*), or quartzitic outcrops (*L. framesii*, *L. patula*), and on shale-derived soils (*L. obscura*, *L. zebrina*). Bulb elevation was not scored as a character as no clearly discontinuous states occurred.

Six bulb characters were defined for the cladistic analyses:

1) **Bulb shape.** Three states occurred: globose (=0); subglobose (=1); and ovoid (=2). Qualitative character, scored as character 1 (Appendix 1).

Bulb shape in *Massonia* was globose. In *Lachenalia* and *Polyxena* this state occurred in 68 (49%) taxa (66 *Lachenalia*, two *Polyxena*) (Figure 3A). In 50 (36%) taxa (47 *Lachenalia*, three *Polyxena*), bulbs had a girth that exceeded their length (termed subglobose in this text) (Figure 3C), and in 21 (15%) *Lachenalia* taxa the bulbs were longer than broad, resulting in ovoid bulb shape (Figure 3B, Table 2).

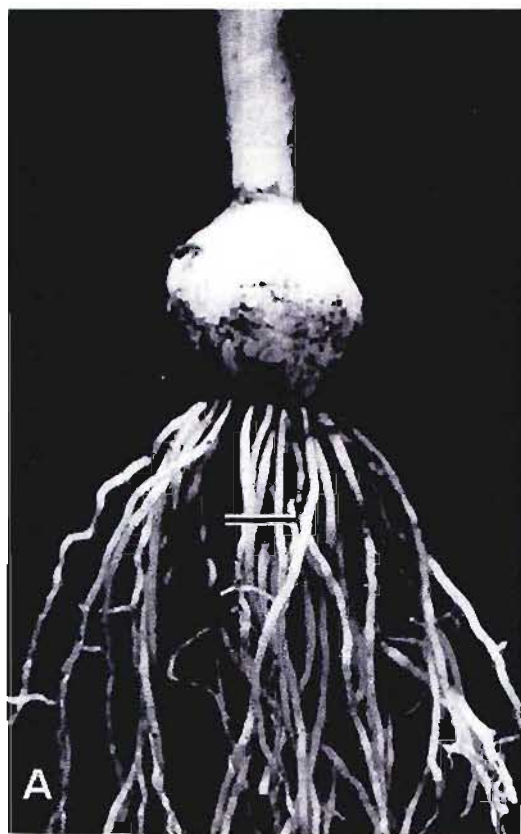


Table 2. Variation in bulb shape in <i>Lachenalia</i>, <i>Polyxena</i> and the outgroup <i>Massonia</i>	
Character State	Taxa
Globose	<i>L. alba</i> , <i>L. algoensis</i> , <i>L. aloides</i> var. <i>aurea</i> , <i>L. aloides</i> var. <i>bonaspei</i> , <i>L. aloides</i> var. <i>luteola</i> , <i>L. aloides</i> var. <i>thunbergii</i> , <i>L. aloides</i> var. <i>vanzyliae</i> , <i>L. ameliae</i> , <i>L. angelica</i> , <i>L. arida</i> , <i>L. barkeriana</i> , <i>L. bolusii</i> , <i>L. canaliculata</i> , <i>L. cernua</i> , <i>L. comptonii</i> , <i>L. concordiana</i> , <i>L. congesta</i> , <i>L. dasybotrya</i> , <i>L. dehoopensis</i> , <i>L. elegans</i> (all four varieties), <i>L. esterhuysenae</i> , <i>L. giessii</i> , <i>L. glauca</i> , <i>L. glaucophylla</i> , <i>L. inconspicua</i> , <i>L. isopetala</i> , <i>L. klinghardtiana</i> , <i>L. lactosa</i> , <i>L. leipoldtii</i> , <i>L. leomontana</i> , <i>L. longibracteata</i> , <i>L. lutea</i> , <i>L. macgregoriorum</i> , <i>L. margaretae</i> , <i>L. marlothii</i> , <i>L. martinae</i> , <i>L. mathewsii</i> , <i>L. mediana</i> var. <i>mediana</i> , <i>L. minima</i> , <i>L. montana</i> , <i>L. muirii</i> , <i>L. multifolia</i> , <i>L. namaquensis</i> , <i>L. neilii</i> , <i>L. nutans</i> , <i>L. obscura</i> , <i>L. orchioides</i> (both varieties), <i>L. patula</i> , <i>L. pearsonii</i> , <i>L. perryae</i> , <i>L. physocaulos</i> , <i>L. polyphylla</i> , <i>L. polypodantha</i> , <i>L. pusilla</i> , <i>L. rubida</i> , <i>L. sargeantii</i> , <i>L. splendida</i> , <i>L. stayneri</i> , <i>L. urceolata</i> , <i>L. wiesei</i> , <i>L. xerophila</i> , <i>L. youngii</i> <i>P. longituba</i> , <i>P. paucifolia</i> <i>Massonia</i>
Subglobose	<i>L. anguinea</i> , <i>L. arbuthnotiae</i> , <i>L. attenuata</i> , <i>L. bachmannii</i> , <i>L. bowkeri</i> , <i>L. bulbifera</i> , <i>L. capensis</i> , <i>L. carnosa</i> , <i>L. contaminata</i> (both varieties), <i>L. convallarioides</i> , <i>L. fistulosa</i> , <i>L. framesii</i> , <i>L. gillettii</i> , <i>L. haarlemensis</i> , <i>L. hirta</i> (both varieties), <i>L. juncifolia</i> (both varieties), <i>L. komsbergensis</i> , <i>L. latimerae</i> , <i>L. liliiflora</i> , <i>L. marginata</i> (both subspecies), <i>L. moniliformis</i> , <i>L. mutabilis</i> , <i>L. nardouwensis</i> , <i>L. nervosa</i> , <i>L. orthopetala</i> , <i>L. peersii</i> , <i>L. purpureocaerulea</i> , <i>L. pustulata</i> , <i>L. reflexa</i> , <i>L. rosea</i> , <i>L. salteri</i> , <i>L. thomasiae</i> , <i>L. trichophylla</i> (both subspecies), <i>L. unicolor</i> , <i>L. unifolia</i> (both varieties), <i>L. valeriae</i> , <i>L. variegata</i> , <i>L. ventricosa</i> , <i>L. viridiflora</i> , <i>L. whitehillensis</i> , <i>L. zeyheri</i> <i>P. corymbosa</i> , <i>P. ensifolia</i> , <i>P. maughanii</i>
Ovoid	<i>L. aloides</i> var. <i>aloides</i> , <i>L. aloides</i> var. <i>piketbergensis</i> , <i>L. aloides</i> var. <i>quadricolor</i> , <i>L. aurioliae</i> , <i>L. buchbergensis</i> , <i>L. campanulata</i> , <i>L. doleritica</i> , <i>L. duncanii</i> , <i>L. fasciculata</i> , <i>L. karooica</i> , <i>L. kliprandensis</i> , <i>L. maximiliani</i> , <i>L. mediana</i> var. <i>rogersii</i> , <i>L. namibiensis</i> , <i>L. nordenstamii</i> , <i>L. schelpei</i> , <i>L. undulata</i> (both subspecies), <i>L. verticillata</i> , <i>L. violacea</i> , <i>L. zebrina</i>

2) **Bulb tissue colour.** Three states occurred: white (=0); yellow (=1); and polymorphic (=2). Qualitative character, scored as character 2 (Appendix 1).

Bulb tissue colour was white in *Massonia* and in 107 (89%) ingroup species (102 *Lachenalia*, all five *Polyxena*). In 12 (10%) *Lachenalia* species (*L. gillettii*, *L. kliprandensis*, *L. liliiflora*, *L. margaretae*, *L. nardouwensis*, *L. orthopetala*, *L. purpureocaerulea*, *L. pustulata*, *L. splendida*, *L. thomasiae*, *L. unicolor* and *L. ventricosa*) bulb tissue was pale to dark yellow, and in one species (*L. carnosa*) the condition was polymorphic within populations (Table 3).

Character State	Species
White	<i>L. alba</i> , <i>L. algoensis</i> , <i>L. aloides</i> (all eight varieties), <i>L. ameliae</i> , <i>L. angelica</i> , <i>L. anguinea</i> , <i>L. arbutnotiae</i> , <i>L. arida</i> , <i>L. attenuata</i> , <i>L. aurioliae</i> , <i>L. bachmannii</i> , <i>L. barkeriana</i> , <i>L. bolusii</i> , <i>L. bowkeri</i> , <i>L. buchbergensis</i> , <i>L. bulbifera</i> , <i>L. campanulata</i> , <i>L. canaliculata</i> , <i>L. capensis</i> , <i>L. cernua</i> , <i>L. comptonii</i> , <i>L. concordiana</i> , <i>L. congesta</i> , <i>L. contaminata</i> (both varieties), <i>L. convallarioides</i> , <i>L. dasybotrya</i> , <i>L. dehoopensis</i> , <i>L. doleritica</i> , <i>L. duncanii</i> , <i>L. elegans</i> (all four varieties), <i>L. esterhuysenae</i> , <i>L. fasciculata</i> , <i>L. fistulosa</i> , <i>L. framesii</i> , <i>L. giessii</i> , <i>L. glauca</i> , <i>L. glaucophylla</i> , <i>L. haarlemensis</i> , <i>L. hirta</i> (both varieties), <i>L. inconspicua</i> , <i>L. isopetala</i> , <i>L. juncifolia</i> (both varieties), <i>L. karooica</i> , <i>L. klinghardtiana</i> , <i>L. komsbergensis</i> , <i>L. lactosa</i> , <i>L. latimeriae</i> , <i>L. leipoldtii</i> , <i>L. leomontana</i> , <i>L. longibracteata</i> , <i>L. lutea</i> , <i>L. macgregoriorum</i> , <i>L. marginata</i> (both subspecies), <i>L. marlothii</i> , <i>L. martinae</i> , <i>L. mathewsii</i> , <i>L. maximiliani</i> , <i>L. mediana</i> (both varieties), <i>L. minima</i> , <i>L. moniliformis</i> , <i>L. montana</i> , <i>L. muirii</i> , <i>L. multifolia</i> , <i>L. mutabilis</i> , <i>L. namaquensis</i> , <i>L. namibiensis</i> , <i>L. neilii</i> , <i>L. nervosa</i> , <i>L. nordenstamii</i> , <i>L. nutans</i> , <i>L. obscura</i> , <i>L. orchioides</i> (both varieties), <i>L. patula</i> , <i>L. pearsonii</i> , <i>L. peersii</i> , <i>L. perryae</i> , <i>L. physocaulos</i> , <i>L. polyphylla</i> , <i>L. polypodantha</i> , <i>L. pusilla</i> , <i>L. reflexa</i> , <i>L. rosea</i> , <i>L. rubida</i> , <i>L. salteri</i> , <i>L. sargeantii</i> , <i>L. schelpei</i> , <i>L. stayneri</i> , <i>L. trichophylla</i> (both subspecies), <i>L. undulata</i> (both subspecies), <i>L. unifolia</i> (both varieties), <i>L. urceolata</i> , <i>L. valeriae</i> , <i>L. variegata</i> , <i>L. verticillata</i> , <i>L. violacea</i> , <i>L. viridiflora</i> , <i>L. whitehillensis</i> , <i>L. wiesei</i> , <i>L. xerophila</i> , <i>L. youngii</i> , <i>L. zebrina</i> , <i>L. zeyheri</i> , <i>P. corymbosa</i> , <i>P. ensifolia</i> , <i>P. longituba</i> , <i>P. maughanii</i> , <i>P. paucifolia</i> , <i>Massonia</i>
Yellow	<i>L. gillettii</i> , <i>L. kliprandensis</i> , <i>L. liliiflora</i> , <i>L. margaretae</i> , <i>L. nardouwensis</i> , <i>L. orthopetala</i> , <i>L. purpureocaerulea</i> , <i>L. pustulata</i> , <i>L. splendida</i> , <i>L. thomasiae</i> , <i>L. unicolor</i> , <i>L. ventricosa</i>
Polymorphic	<i>L. carnosa</i>

When *Lachenalia* bulb tissue was exposed to the sun, the surface usually turned deep purple, as in *L. contaminata* and *L. orthopetala*.

3) **Bulb outer tunic texture.** Tunics adhered to the bulb and had various textures. Two states occurred: hard, pale to dark brown or black cartilaginous layers overlaying membranous inner layers (=0); and pale to dark brown or greyish-brown spongy outer layers overlaying membranous inner layers (=1). Qualitative character, scored as character 5 (Appendix 1).

Hard and cartilaginous bulb outer tunics occurred in *Massonia*, and formed a protective layer. This state also occurred in 20 (17%) *Lachenalia* species from arid or semi-arid habitats, such as *L. schelpei* (Figure 3B). The thickness of this layer varied in widely distributed species

like *L. undulata*, depending on the substrate in which they grew; populations occurring in hard, rocky ground had thicker, harder tunics than those of softer, loamy or sandy soils. In 100 (83%) ingroup species (95 *Lachenalia*, all five *Polyxena*) the outer tunics were spongy (Table 4).

Table 4. Variation in bulb outer tunic texture in <i>Lachenalia</i>, <i>Polyxena</i> and the outgroup <i>Massonia</i>	
Character state	Species
Hard	<i>L. arida</i> , <i>L. bowkeri</i> , <i>L. canaliculata</i> , <i>L. concordiana</i> , <i>L. dasybotrya</i> , <i>L. dehoopensis</i> , <i>L. doleritica</i> , <i>L. duncanii</i> , <i>L. fasciculata</i> , <i>giessii</i> , <i>L. isopetala</i> , <i>L. martinae</i> , <i>L. maximiliani</i> , <i>L. minima</i> , <i>L. namibiensis</i> , <i>L. obscura</i> , <i>L. patula</i> , <i>L. pearsonii</i> , <i>L. undulata</i> (both subspecies), <i>L. urceolata</i> <i>Massonia</i>
Spongy	<i>L. alba</i> , <i>L. algoensis</i> , <i>L. aloides</i> (all eight varieties), <i>L. ameliae</i> , <i>L. angelica</i> , <i>L. anguinea</i> , <i>L. arbutnotiae</i> , <i>L. attenuata</i> , <i>L. aurioliae</i> , <i>L. bachmannii</i> , <i>L. barkeriana</i> , <i>L. bolusii</i> , <i>L. buchubergensis</i> , <i>L. bulbifera</i> , <i>L. campanulata</i> , <i>L. capensis</i> , <i>L. carnosa</i> , <i>L. cernua</i> , <i>L. comptonii</i> , <i>L. congesta</i> , <i>L. contaminata</i> (both varieties), <i>L. convallarioides</i> , <i>L. elegans</i> (all four varieties), <i>L. esterhuysenae</i> , <i>L. fistulosa</i> , <i>L. framesii</i> , <i>L. gillettii</i> , <i>L. glauca</i> , <i>L. glaucophylla</i> , <i>L. haarlemensis</i> , <i>L. hirta</i> (both varieties), <i>L. inconspicua</i> , <i>L. juncifolia</i> (both varieties), <i>L. karooica</i> , <i>L. klinghardtiana</i> , <i>L. kliprandensis</i> , <i>L. komsbergensis</i> , <i>L. lactosa</i> , <i>L. latimerae</i> , <i>L. leipoldtii</i> , <i>L. leomontana</i> , <i>L. liliiflora</i> , <i>L. longibracteata</i> , <i>L. lutea</i> , <i>L. macgregoriorum</i> , <i>L. margaretae</i> , <i>L. marginata</i> (both subspecies), <i>L. marlothii</i> , <i>L. mathewsii</i> , <i>L. mediana</i> (both varieties), <i>L. moniliformis</i> , <i>L. montana</i> , <i>L. muiirii</i> , <i>L. multifolia</i> , <i>L. mutabilis</i> , <i>L. namaquensis</i> , <i>L. nardouwensis</i> , <i>L. neilii</i> , <i>L. nervosa</i> , <i>L. nordenstamii</i> , <i>L. nutans</i> , <i>L. orchioides</i> (both varieties), <i>L. orthopetala</i> , <i>L. peersii</i> , <i>L. perryae</i> , <i>L. physocaulos</i> , <i>L. polyphylla</i> , <i>L. polypodantha</i> , <i>L. purpureocaerulea</i> , <i>L. pusilla</i> , <i>L. pustulata</i> , <i>L. reflexa</i> , <i>L. rosea</i> , <i>L. rubida</i> , <i>L. salteri</i> , <i>L. sargeantii</i> , <i>L. schelpei</i> , <i>L. splendida</i> , <i>L. stayneri</i> , <i>L. thomasiae</i> , <i>L. trichophylla</i> (both subspecies), <i>L. undulata</i> (both subspecies), <i>L. unicolor</i> , <i>L. unifolia</i> (both varieties), <i>L. valeriae</i> , <i>L. variegata</i> , <i>L. ventricosa</i> , <i>L. verticillata</i> , <i>L. violacea</i> , <i>L. viridiflora</i> , <i>L. whitehillensis</i> , <i>L. wiesei</i> , <i>L. xerophila</i> , <i>L. youngii</i> , <i>L. zebrina</i> , <i>L. zeyheri</i> <i>P. corymbosa</i> , <i>P. ensifolia</i> , <i>P. longituba</i> , <i>P. maughanii</i> , <i>P. paucifolia</i>

4) **Bulb apex.** Two states were recognized: apex not extended (=0); and apex extended into a distinct long neck (=1). Qualitative character, scored as character 6 (Appendix 1).

Non-extended bulb apices occurred in *Massonia*. This state also occurred in 104 (87%) ingroup species (99 *Lachenalia*, all five *Polyxena*). In 16 (13%) *Lachenalia* species from arid habitats, the bulb apex was distinctly extended, and was surrounded by spongy or cartilaginous tunics (Table 5).

Character State	Species
Non-extended	<i>L. alba</i> , <i>L. algoensis</i> , <i>L. aloides</i> (all eight varieties), <i>L. angelica</i> , <i>L. anguinea</i> , <i>L. arbutnotiae</i> , <i>L. attenuata</i> , <i>L. aurioliae</i> , <i>L. bachmannii</i> , <i>L. barkeriana</i> , <i>L. bolusii</i> , <i>L. bowkeri</i> , <i>L. buchbergensis</i> , <i>L. bulbifera</i> , <i>L. campanulata</i> , <i>L. canaliculata</i> , <i>L. capensis</i> , <i>L. carnosae</i> , <i>L. cernuae</i> , <i>L. comptonii</i> , <i>L. contaminata</i> (both varieties), <i>L. convallarioides</i> , <i>L. dasybotrya</i> , <i>L. elegans</i> (all four varieties), <i>L. esterhuysenae</i> , <i>L. fistulosa</i> , <i>L. framesii</i> , <i>L. gillettii</i> , <i>L. glauca</i> , <i>L. glaucophylla</i> , <i>L. haarlemensis</i> , <i>L. hirta</i> (both varieties), <i>L. juncifolia</i> (both varieties), <i>L. karooica</i> , <i>L. klinghardtiana</i> , <i>L. kliprandensis</i> , <i>L. komsbergensis</i> , <i>L. lactosa</i> , <i>L. latimeriae</i> , <i>L. leipoldtii</i> , <i>L. leomontana</i> , <i>L. liliiflora</i> , <i>L. longibracteata</i> , <i>L. lutea</i> , <i>L. macgregoriorum</i> , <i>L. margaretae</i> , <i>L. marginata</i> (both subspecies), <i>L. marlothii</i> , <i>L. martinae</i> , <i>L. mathewsii</i> , <i>L. maximiliani</i> , <i>L. mediana</i> (both varieties), <i>L. moniliformis</i> , <i>L. montana</i> , <i>L. muirii</i> , <i>L. multifolia</i> , <i>L. mutabilis</i> , <i>L. namaquensis</i> , <i>L. namibiensis</i> , <i>L. nardouwensis</i> , <i>L. neilii</i> , <i>L. nervosa</i> , <i>L. nutans</i> , <i>L. obscura</i> , <i>L. orchioides</i> (both varieties), <i>L. orthopetala</i> , <i>L. patula</i> , <i>L. pearsonii</i> , <i>L. peersii</i> , <i>L. perryae</i> , <i>L. physocaulos</i> , <i>L. polyphylla</i> , <i>L. polypodantha</i> , <i>L. purpureocaerulea</i> , <i>L. pusilla</i> , <i>L. pustulata</i> , <i>L. reflexa</i> , <i>L. rosea</i> , <i>L. rubida</i> , <i>L. salteri</i> , <i>L. sargeantii</i> , <i>L. schelpei</i> , <i>L. splendida</i> , <i>L. stayneri</i> , <i>L. thomasiae</i> , <i>L. trichophylla</i> (both subspecies), <i>L. unicolor</i> , <i>L. unifolia</i> (both varieties), <i>L. valeriae</i> , <i>L. variegata</i> , <i>L. ventricosa</i> , <i>L. verticillata</i> , <i>L. violacea</i> , <i>L. viridiflora</i> , <i>L. whitehillensis</i> , <i>L. wiesei</i> , <i>L. xerophila</i> , <i>L. youngii</i> , <i>L. zeyheri</i> <i>P. corymbosa</i> , <i>P. ensifolia</i> , <i>P. longituba</i> , <i>P. maughanii</i> , <i>P. paucifolia</i> <i>Massonia</i>
Extended	<i>L. ameliae</i> , <i>L. arida</i> , <i>L. concordiana</i> , <i>L. congesta</i> , <i>L. dehoopensis</i> , <i>L. doleritica</i> , <i>L. duncanii</i> , <i>L. fasciculata</i> , <i>L. giessii</i> , <i>L. inconspicua</i> , <i>L. isopetala</i> , <i>L. minima</i> , <i>L. nordenstamii</i> , <i>L. undulata</i> (both subspecies), <i>L. urceolata</i> , <i>L. zebrina</i>

5) **Bulb apex outer tunics.** Two states occurred: fasciculate apices (=0); and non-fasciculate apices (=1). Qualitative character, scored as character 7 (Appendix 1).

The uppermost portion of the outer tunics of *Massonia* and 26 (22%) *Lachenalia* species from arid or semi-arid areas were fasciculate, producing a cluster of short or long, more or less flat, papery bristles or segments from splitting of the upper part of the outermost tunics, such as in *L. schelpei* (Figure 3B). In 94 (78%) ingroup species (89 *Lachenalia*, all five *Polyxena*), the outer tunics were non-fasciculate apices (Table 6).

Table 6. Variation in bulb apex outer tunics in <i>Lachenalia</i>, <i>Polyxena</i> and the outgroup <i>Massonia</i>	
Character State	Species
Fasciculate	<i>L. alba</i> , <i>L. arida</i> , <i>L. aurioliae</i> , <i>L. bowkeri</i> , <i>L. canaliculata</i> , <i>L. concordiana</i> , <i>L. dasybotrya</i> , <i>L. dehoopensis</i> , <i>L. doleritica</i> , <i>L. duncanii</i> , <i>L. fasciculata</i> , <i>L. giessii</i> , <i>L. inconspicua</i> , <i>L. isopetala</i> , <i>L. karooica</i> , <i>L. martiniae</i> , <i>L. minima</i> , <i>L. namibiensis</i> , <i>L. neilii</i> , <i>L. obscura</i> , <i>L. patula</i> , <i>L. pearsonii</i> , <i>L. schelpei</i> , <i>L. undulata</i> (both subspecies), <i>L. urceolata</i> <i>Massonia</i>
Non-fasciculate	<i>L. algoensis</i> , <i>L. aloides</i> (all eight varieties), <i>L. ameliae</i> , <i>L. angelica</i> , <i>L. anguinea</i> , <i>L. arbuthnotiae</i> , <i>L. attenuata</i> , <i>L. bachmannii</i> , <i>L. barkeriana</i> , <i>L. bolusii</i> , <i>L. buchubergensis</i> , <i>L. bulbifera</i> , <i>L. campanulata</i> , <i>L. capensis</i> , <i>L. carnosae</i> , <i>L. cernua</i> , <i>L. comptonii</i> , <i>L. congesta</i> , <i>L. contaminata</i> (both varieties), <i>L. convallarioides</i> , <i>L. elegans</i> (all four varieties), <i>L. esterhuysenae</i> , <i>L. fistulosa</i> , <i>L. framesii</i> , <i>L. gillettii</i> , <i>L. glauca</i> , <i>L. glaucophylla</i> , <i>L. haarlemensis</i> , <i>L. hirta</i> (both varieties), <i>L. juncifolia</i> (both varieties), <i>L. klinghardtiana</i> , <i>L. kliprandensis</i> , <i>L. komsbergensis</i> , <i>L. lactosa</i> , <i>L. latimerae</i> , <i>L. leipoldtii</i> , <i>L. leomontana</i> , <i>L. liliiflora</i> , <i>L. longibracteata</i> , <i>L. lutea</i> , <i>L. macgregoriorum</i> , <i>L. margaretae</i> , <i>L. marginata</i> (both subspecies), <i>L. marlothii</i> , <i>L. mathewsii</i> , <i>L. maximiliani</i> , <i>L. mediana</i> (both varieties), <i>L. moniliformis</i> , <i>L. montana</i> , <i>L. muirii</i> , <i>L. multifolia</i> , <i>L. mutabilis</i> , <i>L. namaquensis</i> , <i>L. nardouwensis</i> , <i>L. nervosa</i> , <i>L. nordenstamii</i> , <i>L. mutans</i> , <i>L. orchioides</i> (both varieties), <i>L. orthopetala</i> , <i>L. peersii</i> , <i>L. perryae</i> , <i>L. physocaulos</i> , <i>L. polyphylla</i> , <i>L. polypodantha</i> , <i>L. purpureocaerulea</i> , <i>L. pusilla</i> , <i>L. pustulata</i> , <i>L. reflexa</i> , <i>L. rosea</i> , <i>L. rubida</i> , <i>L. salteri</i> , <i>L. sargeantii</i> , <i>L. splendida</i> , <i>L. stayneri</i> , <i>L. thomasiae</i> , <i>L. trichophylla</i> (both subspecies), <i>L. unicolor</i> , <i>L. unifolia</i> (both varieties), <i>L. valeriae</i> , <i>L. variegata</i> , <i>L. ventricosa</i> , <i>L. verticillata</i> , <i>L. violacea</i> , <i>L. viridiflora</i> , <i>L. whitehillensis</i> , <i>L. wiesei</i> , <i>L. xerophila</i> , <i>L. youngii</i> , <i>L. zebrina</i> , <i>L. zeyheri</i> <i>P. corymbosa</i> , <i>P. ensifolia</i> , <i>P. longituba</i> , <i>P. maughanii</i> , <i>P. paucifolia</i>

6) **Leaf bases.** Two states occurred: non-concrescent (=0); and concrescent leaf bases (=1). Qualitative character, scored as character 10 (Appendix 1).

Gamophylly (concrescence) of the thickened leaf bases of the previous growth cycle within the bulb only occurred in two, geoflorous *Lachenalia* species, *L. barkeriana* and *L. pusilla* (Müller-Doblies *et al.* 1987). This character state did not occur in *Massonia* or in *Polyxena* but is convergent in certain species of *Ornithogalum* (Hyacinthaceae) and in *Gethyllis linearis* (Amaryllidaceae) (Müller-Doblies 1983).

5.5 CATAPHYLLS

Tubular, membranous cataphylls occur in *Massonia* and in all species of *Lachenalia* and *Polyxena*. Müller-Doblies *et al.* (1987) reported three cataphylls for *L. pusilla*, but normally only two cataphylls are present in mature bulbs. The first (outermost) cataphyll of the new bulb module usually remains below soil level and disintegrates during senescence of the other aerial parts of the plant (Du Toit *et al.* 2001). The second (inner) cataphyll of the new bulb module extends conspicuously above the bulb and in most species the distal portion is partially exposed early in the growing season. It may be translucent, green or red in colour, but in most species it contains little chlorophyll.

5.5.1 Results

The length of the subterranean and aerial portions of the inner cataphyll were highly variable in *Lachenalia*, even within a population. As an example, the length of the inner cataphylls in a population of *L. rubida* growing at Bloubergstrand on the northern Cape Peninsula was found to vary from 15-50 mm long. The inner cataphyll usually had distinct depressed longitudinal veins and the aerial portion was maculate or immaculate and translucent, but this varied, even within populations.

Two cataphyll characters were defined for the cladistic analyses:

1) **Inner cataphyll apex shape.** Three states occurred: obtuse (=0); acute (=1); and polymorphic (=2). Qualitative character, scored as character 8 (Appendix 1).

Obtuse cataphyll apices occurred in *Massonia*. In the 117 ingroup species investigated, 90 (77 %) species (85 *Lachenalia*, all five *Polyxena*) had obtuse apices, 24 (20.5%) *Lachenalia* species had acute apices, and in three (2.5%) *Lachenalia* species, the character was polymorphic within populations (Table 7).

Character State	Species
Obtuse	<i>L. alba</i> , <i>L. algoensis</i> , <i>L. aloides</i> (all eight varieties), <i>L. ameliae</i> , <i>L. anguinea</i> , <i>L. arbuthnotiae</i> , <i>L. arida</i> , <i>L. attenuata</i> , <i>L. aurioliae</i> , <i>L. bachmannii</i> , <i>L. barkeriana</i> , <i>L. bolusii</i> , <i>L. bowkeri</i> , <i>L. buchbergensis</i> , <i>L. bulbifera</i> , <i>L. capensis</i> , <i>L. carnosae</i> , <i>L. congesta</i> , <i>L. contaminata</i> (both varieties), <i>L. dasybotrya</i> , <i>L. dehoopensis</i> , <i>L. doleritica</i> , <i>L. duncanii</i> , <i>L. fasciculata</i> , <i>L. fistulosa</i> , <i>L. framesii</i> , <i>L. giessii</i> , <i>L. gillettii</i> , <i>L. glauca</i> , <i>L. haarlemensis</i> , <i>L. hirta</i> (both varieties), <i>L. inconspicua</i> , <i>L. isopetala</i> , <i>L. juncifolia</i> (both varieties), <i>L. klinghardtiana</i> , <i>L. kliprandensis</i> , <i>L. komsbergensis</i> , <i>L. lactosa</i> , <i>L. latimerae</i> , <i>L. leomontana</i> , <i>L. liliiflora</i> , <i>L. longibracteata</i> , <i>L. lutea</i> , <i>L. macgregoriorum</i> , <i>L. marginata</i> (both subspecies), <i>L. marlothii</i> , <i>L. martinae</i> , <i>L. mathewsii</i> , <i>L. maximiliani</i> , <i>L. mediana</i> (both varieties), <i>L. moniliformis</i> , <i>L. montana</i> , <i>L. muirii</i> , <i>L. mutabilis</i> , <i>L. namaquensis</i> , <i>L. namibiensis</i> , <i>L. nardouwensis</i> , <i>L. neilii</i> , <i>L. nordenstamii</i> , <i>L. obscura</i> , <i>L. orchioides</i> (both varieties), <i>L. orthopetala</i> , <i>L. patula</i> , <i>L. pearsonii</i> , <i>L. peersii</i> , <i>L. perryae</i> , <i>L. polyphylla</i> , <i>L. rosea</i> , <i>L. rubida</i> , <i>L. salteri</i> , <i>L. sargeantii</i> , <i>L. schelpi</i> , <i>L. splendida</i> , <i>L. stayneri</i> , <i>L. thomasiae</i> , <i>L. trichophylla</i> (both subspecies), <i>L. undulata</i> (both subspecies), <i>L. unifolia</i> (both varieties), <i>L. valeriae</i> , <i>L. variegata</i> , <i>L. ventricosa</i> , <i>L. whitehillensis</i> , <i>L. wiesei</i> , <i>L. zebrina</i> , <i>L. zeyheri</i> <i>P. corymbosa</i> , <i>P. ensifolia</i> , <i>P. longituba</i> , <i>P. maughanii</i> , <i>P. paucifolia</i> <i>Massonia</i>
Acute	<i>L. angelica</i> , <i>L. campanulata</i> , <i>L. canaliculata</i> , <i>L. comptonii</i> , <i>L. concordiana</i> , <i>L. convallarioides</i> , <i>L. elegans</i> (all four varieties), <i>L. esterhuysenae</i> , <i>L. glaucophylla</i> , <i>L. karooica</i> , <i>L. leipoldtii</i> , <i>L. margaretae</i> , <i>L. minima</i> , <i>L. multifolia</i> , <i>L. physocaulos</i> , <i>L. polypodantha</i> , <i>L. purpureocaerulea</i> , <i>L. pusilla</i> , <i>L. pustulata</i> , <i>L. unicolor</i> , <i>L. urceolata</i> , <i>L. verticillata</i> , <i>L. violacea</i> , <i>L. youngii</i>
Polymorphic	<i>L. nervosa</i> , <i>L. reflexa</i> , <i>L. viridiflora</i>

Obtuse cataphyll apices were blunt or rounded, whereas acute apices were pointed.

2) Inner cataphyll adhesion to clasping leaf bases. Three states were defined: non-adhering (=0); adhering (=1); and polymorphic (=2). Qualitative character, scored as character 9 (Appendix 1).

Non-adherent inner cataphylls occurred in *Massonia*. In the 135 ingroup taxa investigated, 60 (44%) *Lachenalia* taxa had non-adherent inner cataphylls, 74 (55%) taxa (69 *Lachenalia*, five *Polyxena*) had adherent cataphylls, and in one taxon (*L. bulbifera*) the character was polymorphic within populations (Table 8).

Table 8. Variation in inner cataphyll adhesion to clasping leaf bases in <i>Lachenalia</i>, <i>Polyxena</i> and the outgroup <i>Massonia</i>	
Character State	Taxa
Non-adhering	<i>L. algoensis</i> , <i>L. aloides</i> var. <i>aloides</i> , <i>L. aloides</i> var. <i>bonaspei</i> , <i>L. aloides</i> var. <i>luteola</i> , <i>L. aloides</i> var. <i>piketbergensis</i> , <i>L. aloides</i> var. <i>quadricolor</i> , <i>L. angelica</i> , <i>L. anguinea</i> , <i>L. arbutnotiae</i> , <i>L. attenuata</i> , <i>L. bachmannii</i> , <i>L. barkeriana</i> , <i>L. bolusii</i> , <i>L. campanulata</i> , <i>L. canaliculata</i> , <i>L. capensis</i> , <i>L. comptonii</i> , <i>L. concordiana</i> , <i>L. contaminata</i> (both varieties), <i>L. convallarioides</i> , <i>L. duncanii</i> , <i>L. elegans</i> (all four varieties), <i>L. fistulosa</i> , <i>L. glauca</i> , <i>L. haarlemensis</i> , <i>L. hirta</i> (both varieties), <i>L. klinghardtiana</i> , <i>L. lactosa</i> , <i>L. liliiflora</i> , <i>L. margaretae</i> , <i>L. marginata</i> (both subspecies), <i>L. marlothii</i> , <i>L. martinae</i> , <i>L. minima</i> , <i>L. moniliformis</i> , <i>L. muirii</i> , <i>L. mutabilis</i> , <i>L. obscura</i> , <i>L. peersii</i> , <i>L. perryae</i> , <i>L. polypodantha</i> , <i>L. rubida</i> , <i>L. splendida</i> , <i>L. stayneri</i> , <i>L. thomasiae</i> , <i>L. undulata</i> (both subspecies), <i>L. unicolor</i> , <i>L. urceolata</i> , <i>L. variegata</i> , <i>L. ventricosa</i> , <i>L. verticillata</i> , <i>L. violacea</i> , <i>L. wiesei</i> <i>Massonia</i>
Adhering	<i>L. alba</i> , <i>L. aloides</i> var. <i>aurea</i> , <i>L. aloides</i> var. <i>thunbergii</i> , <i>L. aloides</i> var. <i>vanzyliae</i> , <i>L. ameliae</i> , <i>L. arida</i> , <i>L. aurioliae</i> , <i>L. bowkeri</i> , <i>L. buchbergensis</i> , <i>L. carnosae</i> , <i>L. congesta</i> , <i>L. dasybotrya</i> , <i>L. dehoopensis</i> , <i>L. doleritica</i> , <i>L. fasciculata</i> , <i>L. framesii</i> , <i>L. giessii</i> , <i>L. gillettii</i> , <i>L. glaucophylla</i> , <i>L. inconspicua</i> , <i>L. isopetala</i> , <i>L. juncifolia</i> (both varieties), <i>L. karooica</i> , <i>L. kliprandensis</i> , <i>L. komsbergensis</i> , <i>L. latimeriae</i> , <i>L. leipoldtii</i> , <i>L. leomontana</i> , <i>L. longibracteata</i> , <i>L. lutea</i> , <i>L. macgregoriorum</i> , <i>L. mathewsii</i> , <i>L. maximiliani</i> , <i>L. mediana</i> (both varieties), <i>L. montana</i> , <i>L. multifolia</i> , <i>L. namaquensis</i> , <i>L. namibiensis</i> , <i>L. nardouwensis</i> , <i>L. neilii</i> , <i>L. nervosa</i> , <i>L. nutans</i> , <i>L. orchioides</i> (both varieties), <i>L. orthopetala</i> , <i>L. patula</i> , <i>L. pearsonii</i> , <i>L. physocaulos</i> , <i>L. polyphylla</i> , <i>L. purpureocaerulea</i> , <i>L. pusilla</i> , <i>L. pustulata</i> , <i>L. reflexa</i> , <i>L. rosea</i> , <i>L. salteri</i> , <i>L. sargeantii</i> , <i>L. schelpei</i> , <i>L. trichophylla</i> (both subspecies), <i>L. unifolia</i> (both varieties), <i>L. valeriae</i> , <i>L. viridiflora</i> , <i>L. whitehillensis</i> , <i>L. youngii</i> , <i>L. zebrina</i> , <i>L. zeyheri</i> <i>P. corymbosa</i> , <i>P. ensifolia</i> , <i>P. longituba</i> , <i>P. maughanii</i> , <i>P. paucifolia</i>
Polymorphic	<i>L. bulbifera</i>

Non-adherent cataphylls loosely surrounded the upper two thirds of the clasping leaf bases, whereas the entire length of adherent cataphylls clung tightly to the clasping leaf bases.

5.6 LEAVES

Leaf morphology in *Lachenalia* is remarkably diverse but does provide useful qualitative and quantitative characters. Leaves in *Massonia* and all species of *Lachenalia* and *Polyxena* are shed annually and are mostly soft and fleshy. Succulence is autapomorphic in *L. patula* (previously known as *L. succulenta*). Xerophytes such as *L. duncanii* and *L. isopetala* have coriaceous leaves (Duncan & Linder Smith 1999a). Leaf shape varies from ovate to linear, leaf number from solitary to rosulate, and leaf orientation from prostrate to erect; most

Lachenalia taxa produce one or two spreading or suberect lanceolate leaves. Adaxial leaf surfaces are usually smooth and immaculate but may be densely maculate, pustulate, or covered with simple or stellate trichomes. Abaxial leaf surfaces are smooth and immaculate but may be densely maculate or covered with simple trichomes (Duncan 1988a).

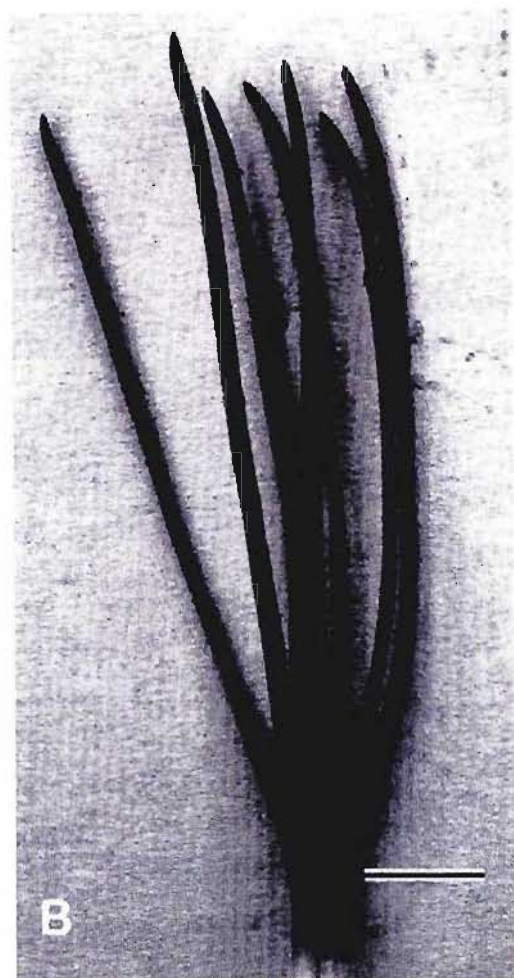
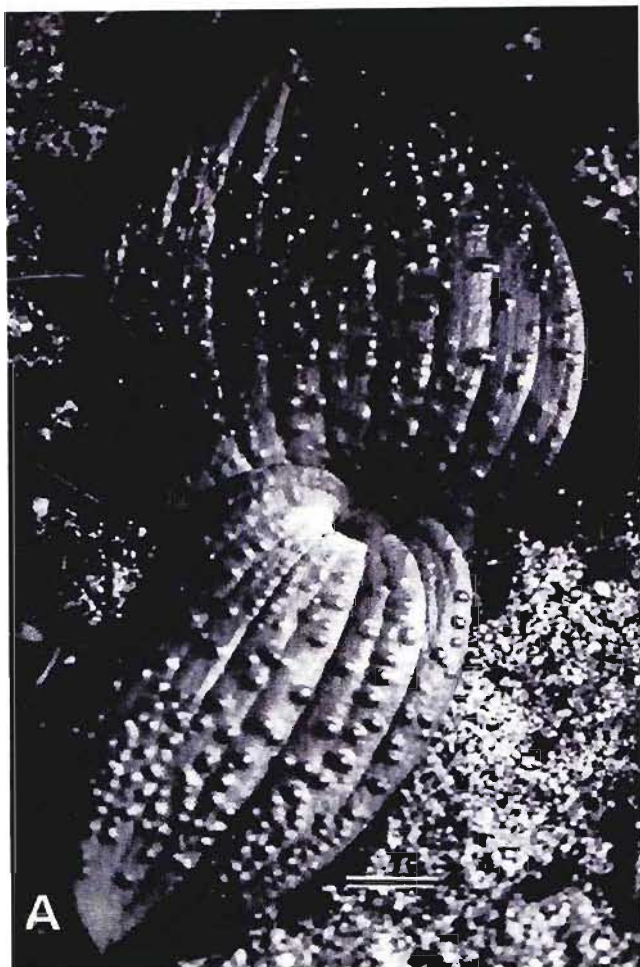
5.6.1 Results

The colour of the adaxial and abaxial lamina surfaces in the outgroup *Massonia*, *Polyxena* and in most *Lachenalia* species varied mainly through shades of pale to dark green. Eight *Lachenalia* species (*L. duncanii*, *L. inconspicua*, *L. karooica*, *L. macgregoriorum*, *L. muirii*, *L. physocaulos*, *L. ventricosa* and *L. violacea*) had greyish-green leaves and eight taxa (*L. buchbergensis*, *L. glaucophylla*, *L. isopetala*, *L. klinghardtiana*, *L. multifolia*, *L. nutans* and *L. undulata* subsp. *undulata* and *L. verticillata*) had glaucous leaves. In five *Lachenalia* species (*L. arbuthnotiae*, *L. capensis*, *L. margaretae*, *L. peersii* and *L. unicolor*) lamina colour was polymorphic, in which adaxial and abaxial lamina surface colour varied from uniformly dark green to partially dark green and dark magenta, or to uniformly dark magenta, within populations. The extremely short, erect leaves of *L. patula* turn bright maroon in bright sunlight and are perfectly camouflaged against the quartz pebbles amongst which it grows. Three *Lachenalia* taxa with prostrate leaves (*L. angelica*, *L. congesta* and *L. trichophylla* subsp. *trichophylla*) had abaxial surfaces that were pale to dark magenta. This coloration was due to anthocyanins present in vacuoles of the subepidermal cell layer. Lamina surface colour was not used as a character in the cladistic analyses as colour differences were frequently insufficiently distinct to form clear cut character states.

Leaf length and width were highly variable. The species with the shortest leaves were *L. angelica* (up to 20 mm) and *L. patula* (up to 30 mm). *L. anguinea* had the longest leaves (up to 320 mm). Leaf length varied greatly across the distribution range of certain widely distributed species like *L. bulbifera* and *L. pusilla*, and there was frequently considerable intrapopulational variation in the leaf length of certain species such as *L. mutabilis* and

L. purpureocaerulea. The leaves of individuals occurring in semi-shaded conditions were usually larger than those which were fully exposed. *L. polyphylla* had the narrowest leaves (0.8-1.0 mm) (Figure 6B), and *L. bulbifera* had the broadest leaves (up to 90 mm) (Figure 11T). Leaf length and width were not used in the cladistic analyses as no clearly discontinuous states could be defined.

Depressed longitudinal grooves occurred between the major veins on the adaxial lamina surfaces of *Massonia* and all *Lachenalia* and *Polyxena* species, to a greater or lesser extent. Those of *L. nervosa* were particularly deep and conspicuous, hence its specific epithet (Figure 6 A).



Under cultivation, liberal watering resulted in the leaves of the proteranthous species remaining green throughout the flowering period. The leaves of two species that are completely deciduous in the wild, *L. campanulata* and *P. longituba*, remained evergreen under cultivation.

Lamina surface and margin anatomy and micromorphology are discussed in Chapter 5.8.

Ten leaf characters were defined for the cladistic analyses:

1) **Leaf base markings.** Three states were defined: immaculate (=0); banded (=1); and spotted (=2). Qualitative character, scored as character 11 (Appendix 1).

The clasping leaf bases of *Massonia* were immaculate. In *Lachenalia* and *Polyxena* 88 (63%) taxa (83 *Lachenalia*, five *Polyxena*) had immaculate clasping leaf bases. In 33 (24%) *Lachenalia* taxa leaf bases were banded (Figure 4A-F), and in 18 (13%) *Lachenalia* taxa they were spotted (Figure 5A-E) (Table 9).

Character State	Taxa
Immaculate	<i>L. alba</i> , <i>L. algoensis</i> , <i>L. aloides</i> var. <i>aloides</i> , <i>L. aloides</i> var. <i>aurea</i> , <i>L. aloides</i> var. <i>bonaspei</i> , <i>L. aloides</i> var. <i>luteola</i> , <i>L. aloides</i> var. <i>piketbergensis</i> , <i>L. aloides</i> var. <i>quadricolor</i> , <i>L. aloides</i> var. <i>thunbergii</i> , <i>L. angelica</i> , <i>L. arida</i> , <i>L. bachmannii</i> , <i>L. barkeriana</i> , <i>L. bowkeri</i> , <i>L. bulbifera</i> , <i>L. capensis</i> , <i>L. carnososa</i> , <i>L. comptonii</i> , <i>L. congesta</i> , <i>L. contaminata</i> (both varieties), <i>L. convallarioides</i> , <i>L. dasybotrya</i> , <i>L. doleritica</i> , <i>L. duncanii</i> , <i>L. elegans</i> var. <i>elegans</i> , <i>L. esterhuysenae</i> , <i>L. fistulosa</i> , <i>L. framesii</i> , <i>L. giessii</i> , <i>L. gillettii</i> , <i>L. glauca</i> , <i>L. glaucophylla</i> , <i>L. isopetala</i> , <i>L. kliprandensis</i> , <i>L. lactosa</i> , <i>L. leomontana</i> , <i>L. liliiflora</i> , <i>L. lutea</i> , <i>L. margaretae</i> , <i>L. mathewsii</i> , <i>L. maximiliani</i> , <i>L. mediana</i> var. <i>mediana</i> , <i>L. minima</i> , <i>L. montana</i> , <i>L. muirii</i> , <i>L. multifolia</i> , <i>L. mutabilis</i> , <i>L. namaquensis</i> , <i>L. namibiensis</i> , <i>L. nardouwensis</i> , <i>L. neilii</i> , <i>L. nervosa</i> , <i>L. nutans</i> , <i>L. orchioides</i> (both varieties), <i>L. orthopetala</i> , <i>L. patula</i> , <i>L. pearsonii</i> , <i>L. peersii</i> , <i>L. physocaulos</i> , <i>L. polyphylla</i> , <i>L. polypodantha</i> , <i>L. purpureocaerulea</i> , <i>L. pusilla</i> , <i>L. pustulata</i> , <i>L. reflexa</i> , <i>L. rosea</i> , <i>L. salteri</i> , <i>L. sargeantii</i> , <i>L. splendida</i> , <i>L. stayneri</i> , <i>L. thomasiae</i> , <i>L. trichophylla</i> (both subspecies), <i>L. undulata</i> (both subspecies), <i>L. unicolor</i> , <i>L. valeriae</i> , <i>L. ventricosa</i> , <i>L. viridiflora</i> , <i>L. xerophila</i> , <i>L. youngii</i> , <i>L. zeyheri</i> <i>P. corymbosa</i> , <i>P. ensifolia</i> , <i>P. longituba</i> , <i>P. maughanii</i> , <i>P. paucifolia</i> <i>Massonia</i>
Banded	<i>L. anguinea</i> , <i>L. attenuata</i> , <i>L. bolusii</i> , <i>L. buchbergensis</i> , <i>L. concordiana</i> , <i>L. dehoopensis</i> , <i>L. fasciculata</i> , <i>L. haarlemensis</i> , <i>L. hirta</i> (both varieties), <i>L. inconspicua</i> , <i>L. juncifolia</i> (both varieties), <i>L. karooica</i> , <i>L. komsbergensis</i> , <i>L. marginata</i> (both subspecies), <i>L. marlothii</i> , <i>L. martinae</i> , <i>L. mediana</i> var. <i>rogersii</i> , <i>L. moniliformis</i> , <i>L. nordenstamii</i> , <i>L. obscura</i> , <i>L. perryae</i> , <i>L. schelpei</i> , <i>L. unifolia</i> (both varieties), <i>L. urceolata</i> , <i>L. verticillata</i> , <i>L. whitehillensis</i> , <i>L. wiesei</i> , <i>L. zebrina</i>
Spotted	<i>L. aloides</i> var. <i>vanzyliae</i> , <i>L. ameliae</i> , <i>L. arbuthnotiae</i> , <i>L. aurioliae</i> , <i>L. campanulata</i> , <i>L. canaliculata</i> , <i>L. cernua</i> , <i>L. elegans</i> var. <i>flava</i> , <i>L. elegans</i> var. <i>membranacea</i> , <i>L. elegans</i> var. <i>suaveolens</i> , <i>L. klinghardtiana</i> , <i>L. latimeriae</i> , <i>L. leipoldtii</i> , <i>L. longibracteata</i> , <i>L. macgregorium</i> , <i>L. rubida</i> , <i>L. variegata</i> , <i>L. violacea</i>

Banded clasping leaf bases had bands of varying lengths which were at least three times as long as their width. Spotted clasping leaf bases had spots that were more or less round.

The occurrence of banding on the clasping leaf bases and lower region of the abaxial lamina surface was particularly evident (but not restricted to) species with single linear leaves, such as *L. hirta* and *L. unifolia* (Figure 4 A,D).



Figure 4. Variation in banding of clasp leaf bases in *Lachenalia*. A, *L. hirta* var. *hirta* (Duncan 77); B, *L. whitehillensis* (Duncan 242); C, *L. zebrina* (Thomas 272); D, *L. unifolia* var. *unifolia* (Duncan 253); E, *L. bolusii* (Duncan 256); F, *L. moniliformis* (Perry 795). Scale bar = 20 mm.

In *L. zebrina*, the abaxial lamina and aerial portion of the clasp leaf base was marked with broad, dark purple transverse bands, shading to dark magenta at ground level and to bright magenta on the subterranean portion of the clasp leaf base, whereas the adaxial lamina was always immaculate. In *L. anguinea*, the abaxial lamina was banded with narrow, bright green transverse bands, shading to magenta on the clasp leaf base and the subterranean portion of the clasp leaf base. In *L. campanulata* the clasp leaf base was marked with minute spots only 1-2 mm in diam., whereas in *L. klinghardtiana* the spots were large and up to 6 mm in diam. (Figure 5 B,E).

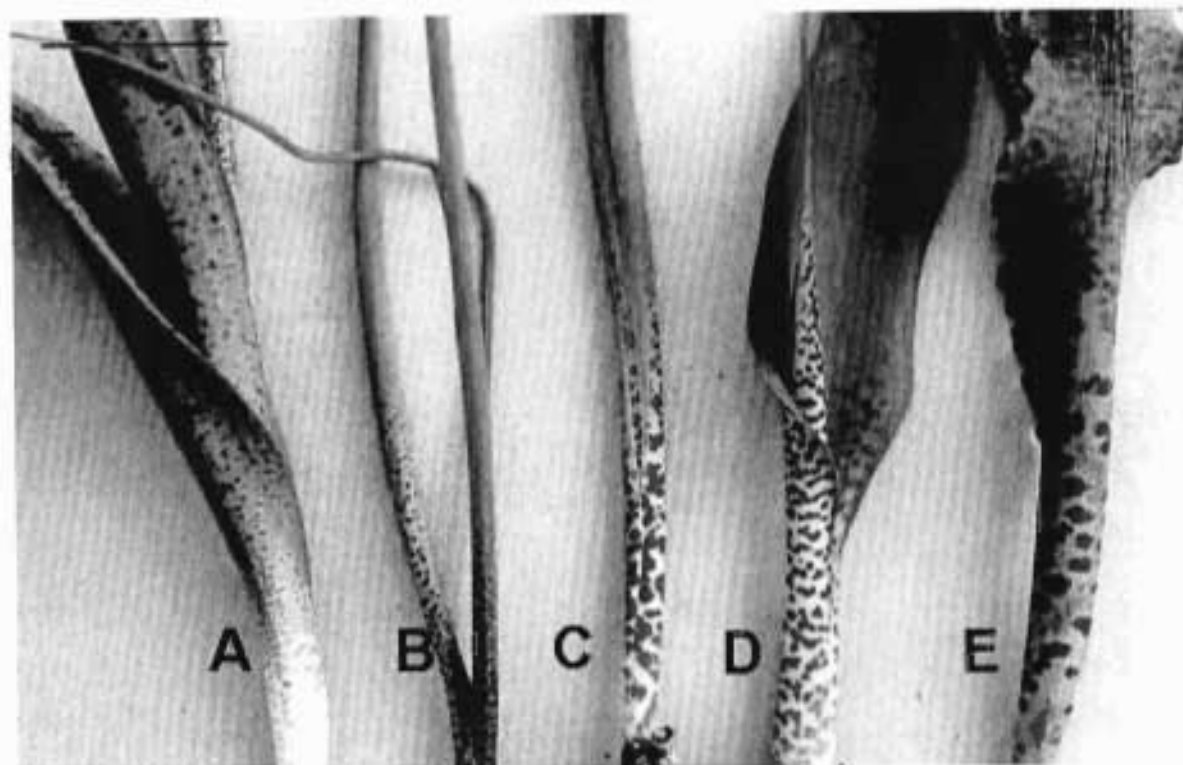


Figure 5. Variation in spotting of clasping leaf bases in *Lachenalia*. A, *L. aurioliae* (Duncan 394); B, *L. campanulata* (Duncan 403); C, *L. latimeriae* (Vorster 3028); D, *L. variegata* (Duncan 392); E, *L. klinghardtiana* (Duncan 118).
Scale bar = 20 mm.

2) **Leaf number.** Five states were defined: always two (=0); always solitary (=1); one or two (=2); two or more (=3); and three or more (=4). Quantitative character, scored as character 12 (Appendix 1).

Massonia always had two leaves per adult bulb, as did 37 (31%) ingroup species (34 *Lachenalia*, three *Polyxena*). In *Lachenalia* and *Polyxena* 42 (35 %) species (41 *Lachenalia*, one *Polyxena*) produced single and two-leaved individuals within single populations, and 33 (27%) *Lachenalia* species always produced solitary leaves. A single *Polyxena* species (*P. corymbosa*) produced two or more leaves within populations, and seven (6%) *Lachenalia* species always had three or more leaves (Table 10).

Character State	Species
Always two	<i>L. alba</i> , <i>L. algoensis</i> , <i>L. aloides</i> (all eight varieties), <i>L. arida</i> , <i>L. bachmannii</i> , <i>L. campanulata</i> , <i>L. carnosae</i> , <i>L. congesta</i> , <i>L. dasybotrya</i> , <i>L. doleritica</i> , <i>L. duncanii</i> , <i>L. giessii</i> , <i>L. isopetala</i> , <i>L. juncifolia</i> (both varieties), <i>L. kliprandensis</i> , <i>L. liliiflora</i> , <i>L. macgregorium</i> , <i>L. mathewsii</i> , <i>L. minima</i> , <i>L. montana</i> , <i>L. muirii</i> , <i>L. nardouwensis</i> , <i>L. neilii</i> , <i>L. nervosa</i> , <i>L. patula</i> , <i>L. pearsonii</i> , <i>L. purpureocaerulea</i> , <i>L. sargeantii</i> , <i>L. schelpei</i> , <i>L. stayneri</i> , <i>L. undulata</i> (both subspecies), <i>L. unicolor</i> , <i>L. urceolata</i> , <i>L. youngii</i> <i>P. ensifolia</i> , <i>P. longituba</i> , <i>P. maughanii</i> <i>Massonia</i>
Always solitary	<i>L. angelica</i> , <i>L. anguinea</i> , <i>L. attenuata</i> , <i>L. bolusii</i> , <i>L. buchbergensis</i> , <i>L. concordiana</i> , <i>L. convallarioides</i> , <i>L. fasciculata</i> , <i>L. glaucophylla</i> , <i>L. haarlemensis</i> , <i>L. hirta</i> (both varieties), <i>L. inconspicua</i> , <i>L. klinghardtiana</i> , <i>L. komsbergensis</i> , <i>L. leipoldtii</i> , <i>L. leomontana</i> , <i>L. marginata</i> (both subspecies), <i>L. marlothii</i> , <i>L. martiniae</i> , <i>L. maximiliani</i> , <i>L. mutabilis</i> , <i>L. nordenstamii</i> , <i>L. nutans</i> , <i>L. perryae</i> , <i>L. physocaulos</i> , <i>L. polypodantha</i> , <i>L. trichophylla</i> (both subspecies), <i>L. unifolia</i> (both varieties), <i>L. ventricosa</i> , <i>L. verticillata</i> , <i>L. whitehillensis</i> , <i>L. wiesei</i> , <i>L. zebrina</i>
One or two	<i>L. ameliae</i> , <i>arbuthnotiae</i> , <i>L. aurioliae</i> , <i>L. bowkeri</i> , <i>L. bulbifera</i> , <i>L. canaliculata</i> , <i>L. capensis</i> , <i>L. cernua</i> , <i>L. comptonii</i> , <i>L. dehoopensis</i> , <i>elegans</i> (all four varieties), <i>L. esterhuysenae</i> , <i>L. fistulosa</i> , <i>L. framesii</i> , <i>L. gillettii</i> , <i>L. glauca</i> , <i>L. karooica</i> , <i>L. lactosa</i> , <i>L. latimerae</i> , <i>L. longibracteata</i> , <i>L. lutea</i> , <i>L. margaretae</i> , <i>L. mediana</i> (both varieties), <i>L. namaquensis</i> , <i>L. namibiensis</i> , <i>L. obscura</i> , <i>L. orchioides</i> (both varieties), <i>L. peersii</i> , <i>L. pustulata</i> , <i>L. reflexa</i> , <i>L. rosea</i> , <i>L. rubida</i> , <i>L. salteri</i> , <i>L. splendida</i> , <i>L. thomasiae</i> , <i>L. valeriae</i> , <i>L. variegata</i> , <i>L. violacea</i> , <i>L. viridiflora</i> , <i>L. xerophila</i> , <i>L. zeyheri</i> <i>P. paucifolia</i>
Two or more	<i>P. corymbosa</i>
Three or more	<i>L. barkeriana</i> , <i>L. contaminata</i> (both varieties), <i>L. moniliformis</i> , <i>L. multifolia</i> , <i>L. orthopetala</i> , <i>L. polyphylla</i> , <i>L. pusilla</i>

With the exception of *L. pusilla* that had lanceolate leaves, the multi-leafed species produced linear leaves. Among these, the highest number of leaves counted in an adult bulb was 18 leaves for *L. multifolia*.

3) **Leaf orientation.** Three states were defined: prostrate (=0), spreading to suberect (=1), and erect (=2). Quantitative character, scored as character 13 (Appendix 1).

Prostrate leaves occurred in *Massonia*, as well as in seven (6%) *Lachenalia* species (*L. angelica*, *L. congesta*, *L. kliprandensis*, *L. nervosa*, *L. pusilla*, *L. stayneri* and *L. trichophylla*).

In *Lachenalia* and *Polyxena* 107 (89%) species (102 *Lachenalia*, five *Polyxena*) had spreading or suberect leaves (angle of 10-60 degrees from the ground), and six (5%) *Lachenalia* species had erect leaves (angle of 75-90 degrees from the ground), *L. contaminata*, *L. haarlemensis*, *L. moniliformis*, *L. multifolia*, *L. patula* and *L. polyphylla* (Figures 6, 7).

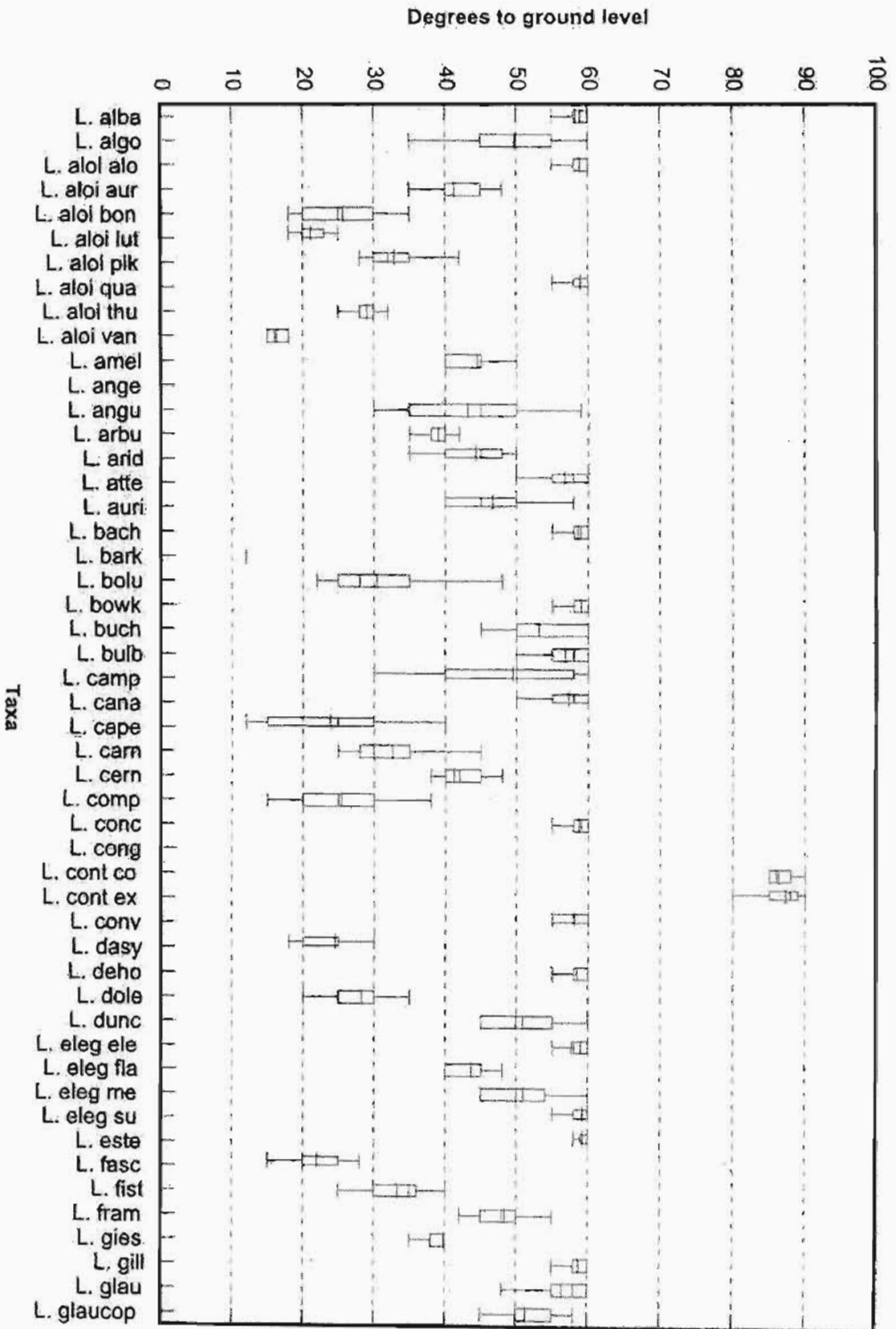


Figure 7. Adult leaf orientation in *Lachenalia* and *Polyxena*

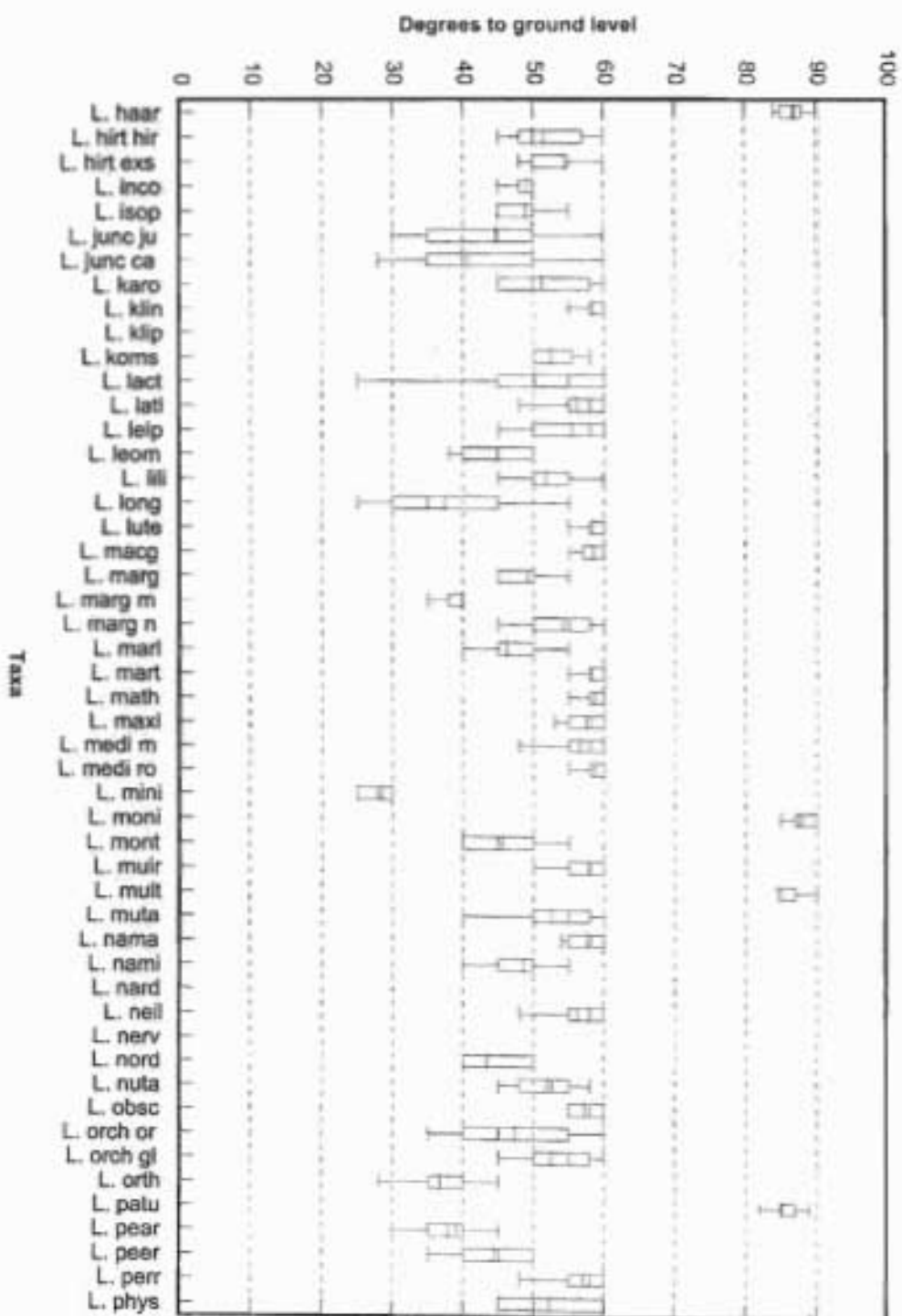


Figure 7. Adult leaf orientation in *Lachenalia* and *Polyxena*

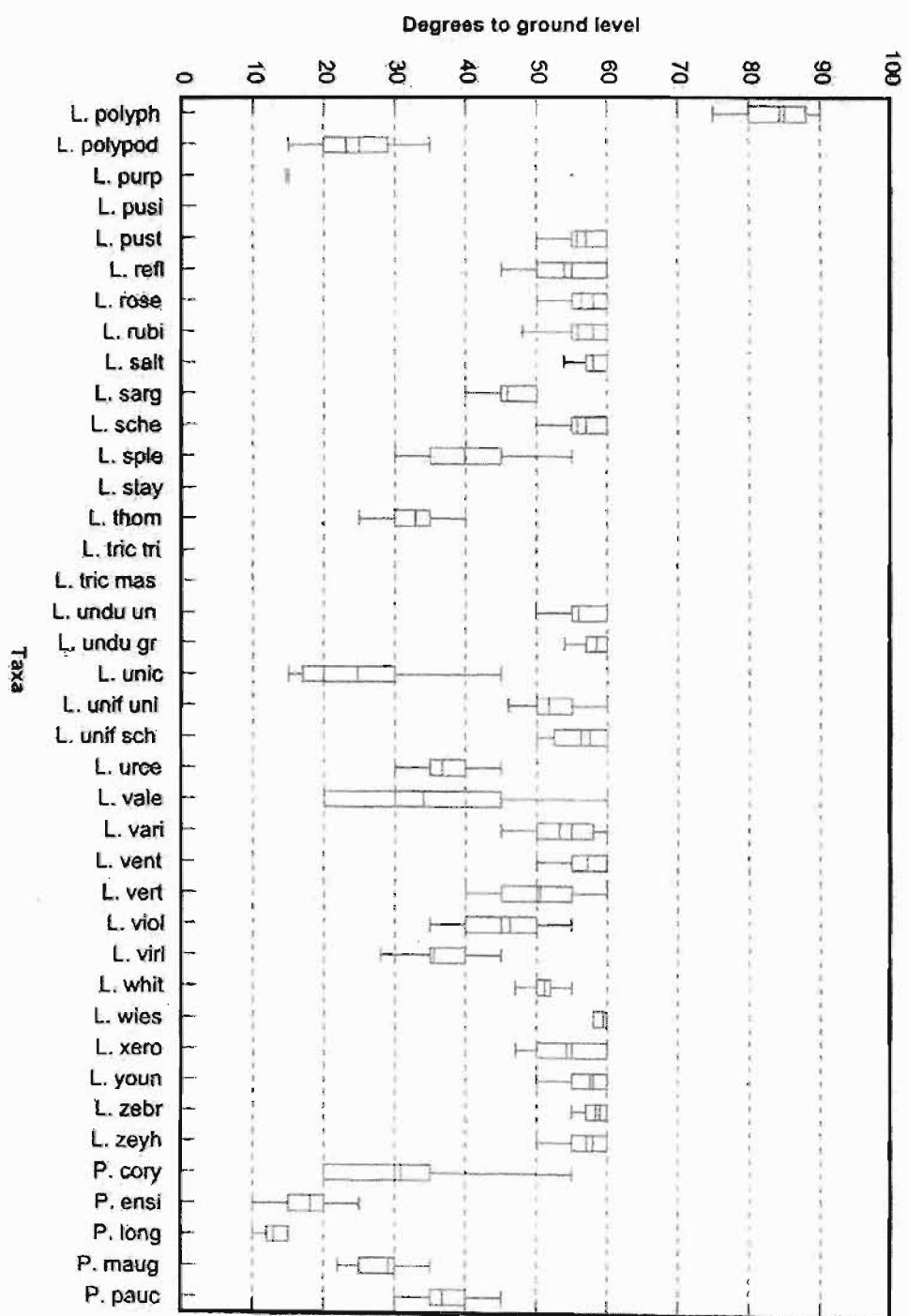


Figure 7. Adult leaf orientation in *Lachenalia* and *Polyxena*

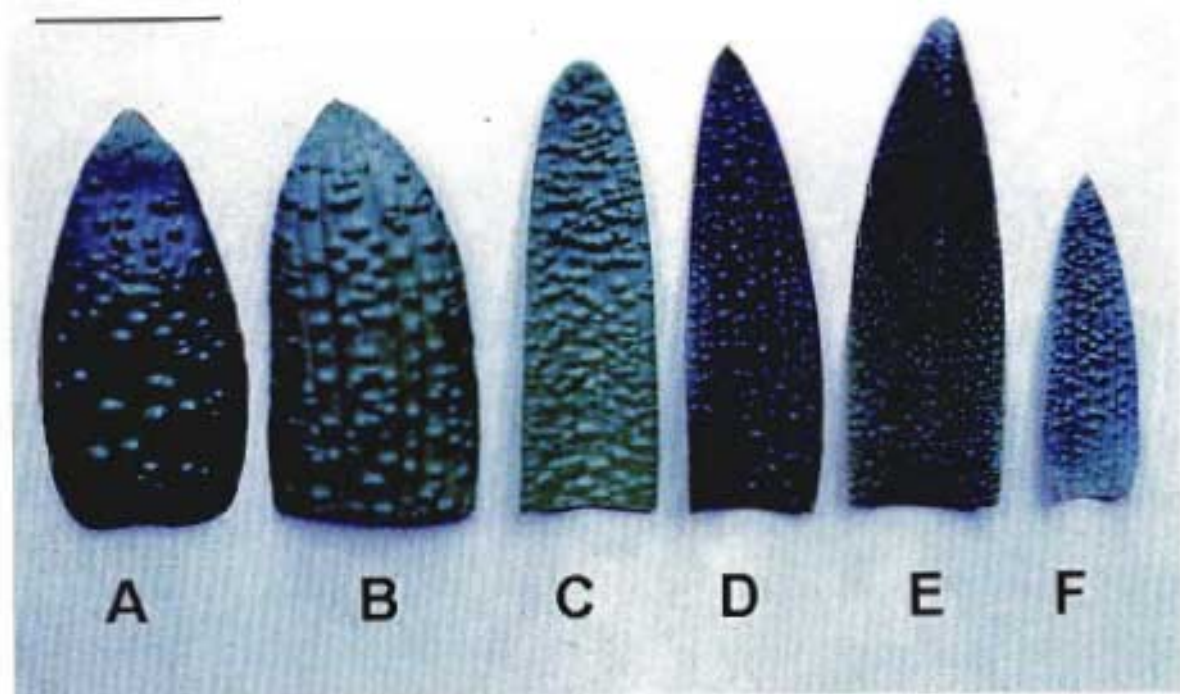


Figure 8. Variation in pustule size and density in *Lachenalia*. A, *L. stayneri* (Stayner s.n.); B, *L. nervosa* (Thomas s.n.); C, *L. pustulata* (Duncan 411); D, *L. liliiflora* (Duncan 434); E, *L. unicolor* (Duncan 66); F, *L. valeriae* (Duncan 444). Scale bar = 30 mm.

Leaf orientation was phenotypically plastic as the prostrate leaf state frequently became spreading or suberect where insufficiently high light levels existed under cultivation.

4) Pustulate/non-pustulate adaxial leaf surface. Three states were defined: non-pustulate (=0); pustules always present (=1); and polymorphic (=2). Qualitative character, scored as character 14 (Appendix 1).

Non-pustulate leaves occurred in *Massonia*, as well as in 111 (92.5%) ingroup species (106 *Lachenalia*, five *Polyxena*). In six (5%) *Lachenalia* species the leaves were always pustulate (*L. liliiflora*, *L. minima*, *L. purpureocaerulea*, *L. stayneri*, *L. unicolor* and *L. valeriae*) (Figure 8). In three (2.5%) *Lachenalia* species pustule presence/absence was polymorphic within populations (*L. carnosae*, *L. nervosa* and *L. pustulata*).

Pustules were usually dome-shaped and their size and density was highly variable, ranging from a sparse to moderate or dense covering of minute pustules 0.5-1.0 mm in diam., such as *L. valeriae* (Figure 8 F), to a moderate or dense covering of medium-sized pustules 1.4-1.7 mm in diam., such as *L. pustulata* and *L. liliiflora* (Figure 8 C,D), or a sporadic, moderate or dense covering of large pustules 2-4 mm in diam., such as *L. stayneri* and *L. nervosa* (Figure 8 A,B). Pustules only occurred on adaxial lamina surfaces, and varied through shades of green, brown or deep purple. The anatomy of pustules was consistent in the genus and comprised elongation of palisade chlorenchyma cells (Figure 9).

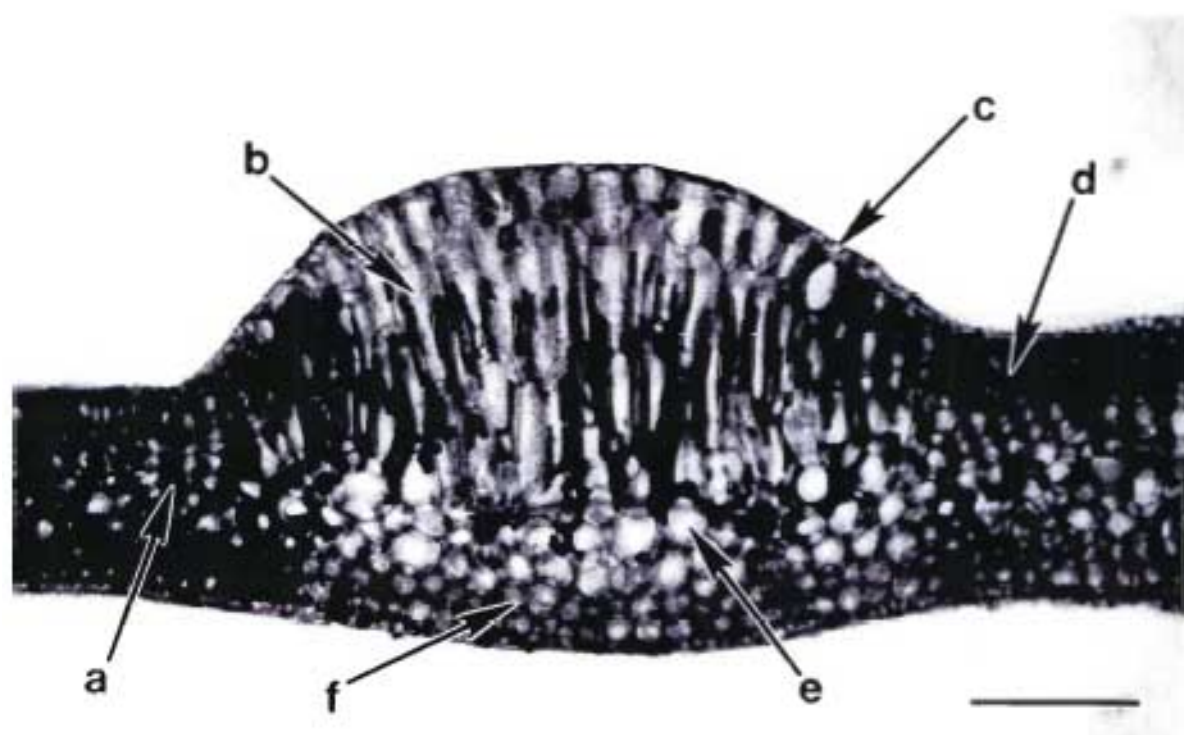


Figure 9. Pustule anatomy in *Lachenalia*. Transverse section through a pustule of *L. minima* (Duncan 171). a = vascular bundle; b = adaxial palisade chlorenchyma; c = adaxial epidermis; d = adaxial chlorenchyma; e = spongy parenchyma; f = abaxial chlorenchyma. Scale bar = 300 μ m.

L. moniliformis produced unique circular, raised fleshy bands along the upper two thirds of their leaves, giving them the appearance of a string of beads, hence the specific epithet *moniliformis*.

5) **Adaxial leaf maculation.** Three states were defined: upper leaf surface always immaculate (=0); upper leaf surface always maculate (=1); and upper leaf surface polymorphic (=2). Qualitative character, scored as character 16 (Appendix 1).

Immaculate upper leaf surfaces occurred in *Massonia*. In *Lachenalia* and *Polyxena*, 92 (66%) taxa (87 *Lachenalia*, five *Polyxena*) had immaculate upper leaf surfaces, 26 (19%) *Lachenalia* taxa always had maculate leaves and in 21 (15%) *Lachenalia* taxa the condition was polymorphic (Figure 10, Table 11).

Character State	Taxa
Always immaculate	<i>L. alba</i> , <i>L. aloides</i> var. <i>piketbergensis</i> , <i>L. aloides</i> var. <i>thunbergii</i> , <i>L. ameliae</i> , <i>L. angelica</i> , <i>L. anguinea</i> , <i>L. arida</i> , <i>L. attenuata</i> , <i>L. bachmannii</i> , <i>L. barkeriana</i> , <i>L. bolusii</i> , <i>L. bowkeri</i> , <i>L. buchbergensis</i> , <i>L. canaliculata</i> , <i>L. comptonii</i> , <i>L. concordiana</i> , <i>L. congesta</i> , <i>L. contaminata</i> var. <i>exserta</i> , <i>L. convallarioides</i> , <i>L. dasybotrya</i> , <i>L. dehoopensis</i> , <i>L. elegans</i> var. <i>elegans</i> , <i>L. elegans</i> var. <i>suaveolens</i> , <i>L. esterhuysenae</i> , <i>L. framesii</i> , <i>L. giessii</i> , <i>L. gillettii</i> , <i>L. glauca</i> , <i>L. glaucophylla</i> , <i>L. haarlemensis</i> , <i>L. hirta</i> (both varieties), <i>L. isopetala</i> , <i>L. juncifolia</i> (both varieties), <i>L. klinghardtiana</i> , <i>L. komsbergensis</i> , <i>L. lactosa</i> , <i>L. latimerae</i> , <i>L. leipoldtii</i> , <i>L. liliiflora</i> , <i>L. lutea</i> , <i>L. macgregoriorum</i> , <i>L. marlothii</i> , <i>L. martinae</i> , <i>L. mathewsii</i> , <i>L. maximiliani</i> , <i>L. mediana</i> (both varieties), <i>L. minima</i> , <i>L. muirii</i> , <i>L. moniliformis</i> , <i>L. montana</i> , <i>L. multifolia</i> , <i>L. mutabilis</i> , <i>L. namaquensis</i> , <i>L. namibiensis</i> , <i>L. nervosa</i> , <i>L. nordenstamii</i> , <i>L. nutans</i> , <i>L. patula</i> , <i>L. pearsonii</i> , <i>L. peersii</i> , <i>L. perryae</i> , <i>L. physocaulos</i> , <i>L. polyphylla</i> , <i>L. polypodantha</i> , <i>L. purpureocaerulea</i> , <i>L. pustulata</i> , <i>L. sargeantii</i> , <i>L. splendida</i> , <i>L. stayneri</i> , <i>L. thomasiae</i> , <i>L. trichophylla</i> (both subspecies), <i>L. undulata</i> subsp. <i>grandifolia</i> , <i>L. unicolor</i> , <i>L. unifolia</i> (both varieties), <i>L. urceolata</i> , <i>L. valeriae</i> , <i>L. ventricosa</i> , <i>L. whitehillensis</i> , <i>L. wiesei</i> , <i>L. xerophila</i> , <i>L. youngii</i> , <i>L. zebrina</i> , <i>L. zeyheri</i> <i>P. corymbosa</i> , <i>P. ensifolia</i> , <i>P. longituba</i> , <i>P. maughanii</i> , <i>P. paucifolia</i> <i>Massonia</i>
Always maculate	<i>L. aloides</i> var. <i>aurea</i> , <i>L. aloides</i> var. <i>bonaspei</i> , <i>L. aloides</i> var. <i>vanzyliae</i> , <i>L. arbuthnotiae</i> , <i>L. aurioliae</i> , <i>L. cernua</i> , <i>L. contaminata</i> var. <i>contaminata</i> , <i>L. elegans</i> var. <i>flava</i> , <i>L. elegans</i> var. <i>membranacea</i> , <i>L. fasciculata</i> , <i>L. inconspicua</i> , <i>L. karooica</i> , <i>L. kliprandensis</i> , <i>L. leomontana</i> , <i>L. longibracteata</i> , <i>L. marginata</i> (both subspecies), <i>L. muirii</i> , <i>L. nardouwensis</i> , <i>L. obscura</i> , <i>L. orchioides</i> (both varieties), <i>L. pusilla</i> , <i>L. rubida</i> , <i>L. schelpei</i> , <i>L. undulata</i> subsp. <i>undulata</i>
Polymorphic	<i>L. algoensis</i> , <i>L. aloides</i> var. <i>aloides</i> , <i>L. aloides</i> var. <i>luteola</i> , <i>L. aloides</i> var. <i>quadricolor</i> , <i>L. bulbifera</i> , <i>L. campanulata</i> , <i>L. capensis</i> , <i>L. carnosa</i> , <i>L. doleritica</i> , <i>L. duncanii</i> , <i>L. fistulosa</i> , <i>L. margaretae</i> , <i>L. neilii</i> , <i>L. orthopetala</i> , <i>L. reflexa</i> , <i>L. rosea</i> , <i>L. salteri</i> , <i>L. variegata</i> , <i>L. verticillata</i> , <i>L. violacea</i> , <i>L. viridiflora</i>

Maculation was produced by a single layer due to the irregular occurrence of anthocyanins in vacuoles of hypodermal cells. In 21 *Lachenalia* taxa, the condition was polymorphic as expression varied within populations, as in *L. viridiflora* (Barker 1972, 1979b). Maculation occurred as spots or blotches, or a combination of these (Figure 10).

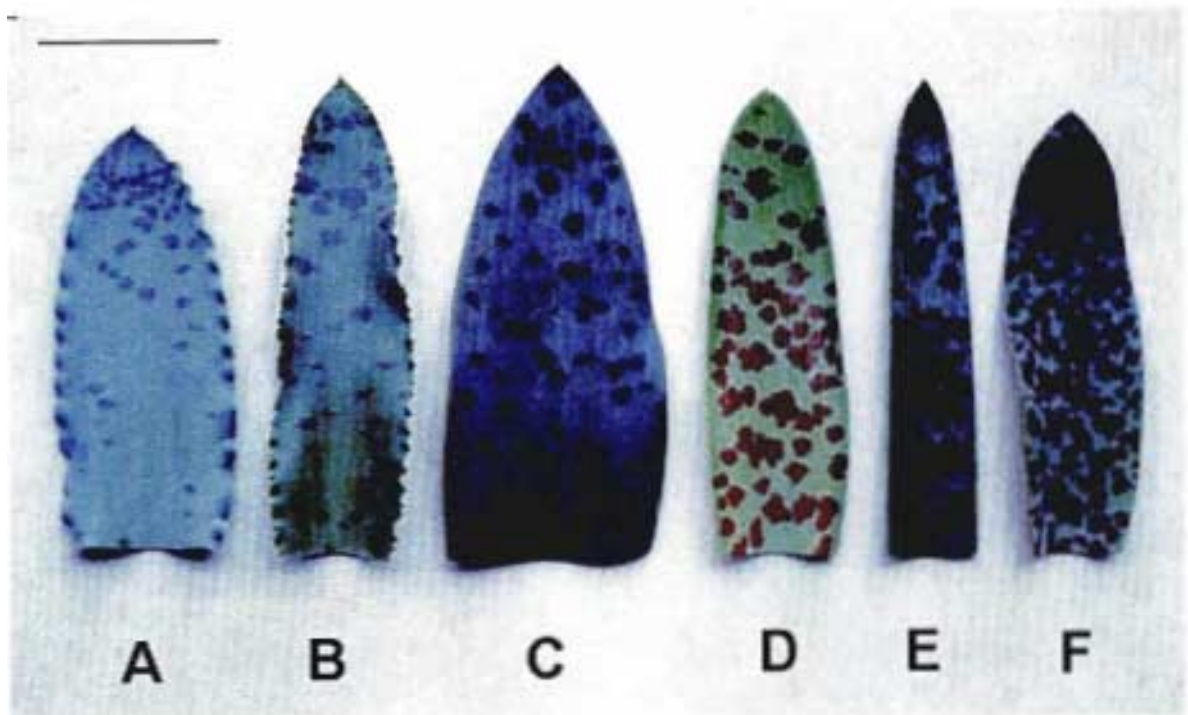


Figure 10. Variation in adaxial leaf maculation in *Lachenalia*.

A, *L. violacea* (Duncan 254); B, *L. duncanii* (Duncan 189);

C, *L. rubida* (Duncan 85); D, *L. arbuthnotiae* (Duncan 393);

E, *L. rosea* (Crous 240); F, *L. orchioides* var. *orchioides* (Duncan 130).

Scale bar = 30 mm.

Spot colour varied through shades of pale to dark purple, magenta, brown or green. Frequently all four colours were present in different parts of the same leaf. Spot colour was also highly variable in some species such as *L. bulbifera* and *L. rubida*, where individuals had leaves with only dark green spots or only dark purple spots within the same population. In *L. arbuthnotiae*, the adaxial lamina was usually heavily spotted with deep purple, with only sporadic spots on the abaxial lamina (Duncan 1988b).

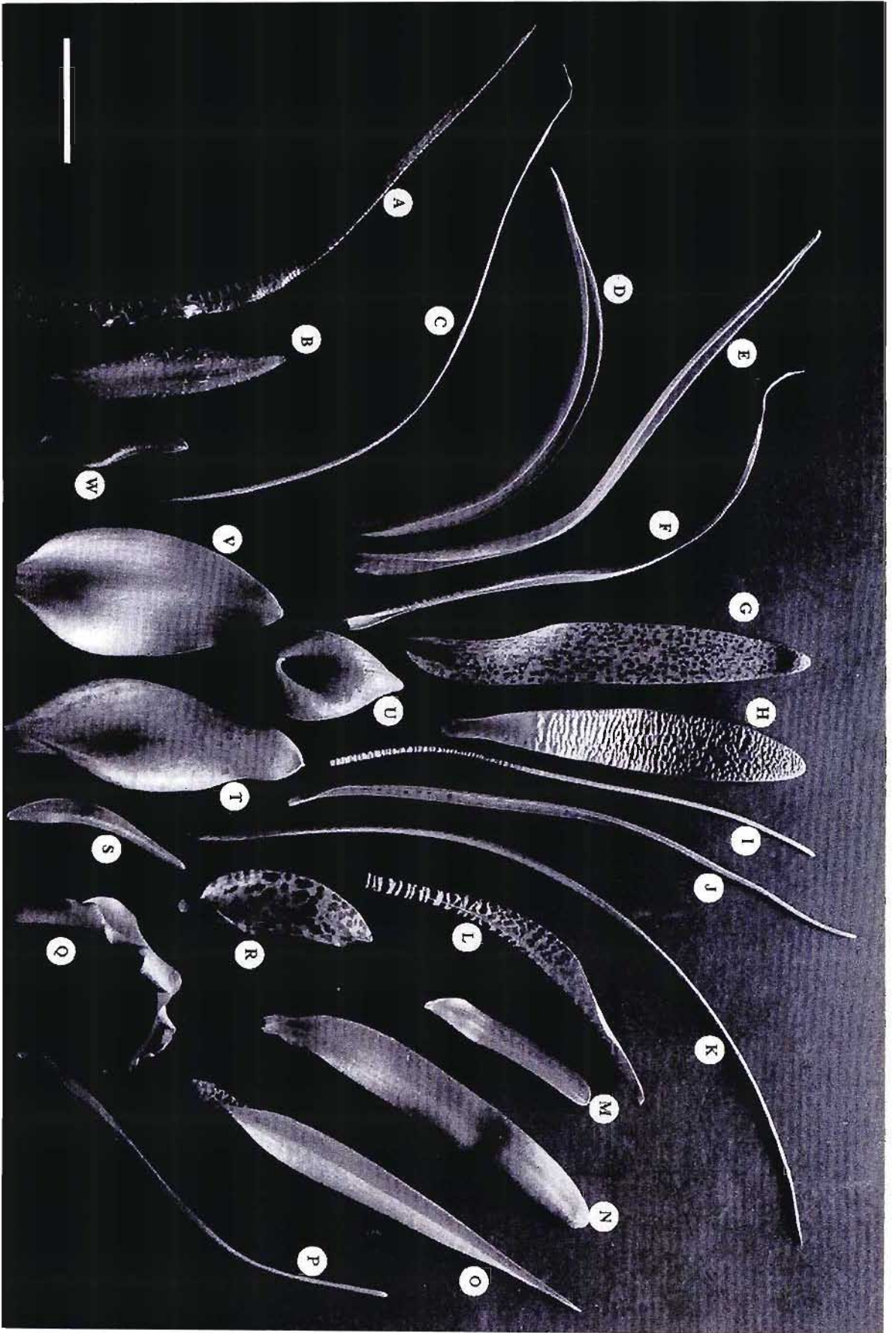
6) **Leaf shape.** Three basic lamina shapes dominated the genus: ovate (=0); lanceolate (=1); and linear leaves (=2). Qualitative character, scored as character 17 (Appendix 1).

Ovate leaves occurred in *Massonia* and 11 (8%) *Lachenalia* taxa. In 99 (71%) ingroup taxa (96 *Lachenalia*, three *Polyxena*) leaves were lanceolate, and in 29 (21%) of the taxa (27 *Lachenalia*, two *Polyxena*) leaves were linear (Figure 11, Table 12).

Character State	Taxa
Ovate	<i>L. bulbifera</i> , <i>L. carnososa</i> , <i>L. congesta</i> , <i>L. dasybotrya</i> , <i>L. doleritica</i> , <i>L. fasciculata</i> , <i>L. kliprandensis</i> , <i>L. marginata</i> subsp. <i>marginata</i> , <i>L. nervosa</i> , <i>L. trichophylla</i> (both subspecies) <i>Massonia</i>
Lanceolate	<i>L. alba</i> , <i>L. algoensis</i> , <i>L. aloides</i> (all eight varieties), <i>L. ameliae</i> , <i>L. angelica</i> , <i>L. anguinea</i> , <i>L. arbutnotiae</i> , <i>L. aurioliae</i> , <i>L. bolusii</i> , <i>L. bowkeri</i> , <i>L. buchbergensis</i> , <i>L. canaliculata</i> , <i>L. capensis</i> , <i>L. cernua</i> , <i>L. comptonii</i> , <i>L. concordiana</i> , <i>L. convallarioides</i> , <i>L. duncanii</i> , <i>L. elegans</i> (all four varieties), <i>L. fistulosa</i> , <i>L. framesii</i> , <i>L. giessii</i> , <i>L. gillettii</i> , <i>L. glauca</i> , <i>L. glaucophylla</i> , <i>L. haarlemensis</i> , <i>L. inconspicua</i> , <i>L. isopetala</i> , <i>L. karooica</i> , <i>L. klinghardtiana</i> , <i>L. komsbergensis</i> , <i>L. lactosa</i> , <i>L. latimerae</i> , <i>L. leipoldtii</i> , <i>L. leomontana</i> , <i>L. liliiflora</i> , <i>L. longibracteata</i> , <i>L. lutea</i> , <i>L. macgregoriorum</i> , <i>L. margaretae</i> , <i>L. marginata</i> subsp. <i>neglecta</i> , <i>L. marlothii</i> , <i>L. martinae</i> , <i>L. maximiliani</i> , <i>L. mediana</i> (both varieties), <i>L. minima</i> , <i>L. muirii</i> , <i>L. mutabilis</i> , <i>L. namibiensis</i> , <i>L. nardouwensis</i> , <i>L. neilii</i> , <i>L. nordenstamii</i> , <i>L. nutans</i> , <i>L. obscura</i> , <i>L. orchioides</i> (both varieties), <i>L. peersii</i> , <i>L. perryae</i> , <i>L. physocaulos</i> , <i>L. polypodantha</i> , <i>L. purpureocaerulea</i> , <i>L. pusilla</i> , <i>L. pustulata</i> , <i>L. reflexa</i> , <i>L. rosea</i> , <i>L. rubida</i> , <i>L. salteri</i> , <i>L. schelpei</i> , <i>L. splendida</i> , <i>L. stayneri</i> , <i>L. thomasiae</i> , <i>L. undulata</i> (both subspecies), <i>L. unicolor</i> , <i>L. urceolata</i> , <i>L. valeriae</i> , <i>L. variegata</i> , <i>L. ventricosa</i> , <i>L. verticillata</i> , <i>L. violacea</i> , <i>L. viridiflora</i> , <i>L. whitehillensis</i> , <i>L. wiesei</i> , <i>L. xerophila</i> , <i>L. zebrina</i> <i>P. ensifolia</i> , <i>P. longituba</i> , <i>P. maughanii</i>
Linear	<i>L. arida</i> , <i>L. attenuata</i> , <i>L. bachmannii</i> , <i>L. barkeriana</i> , <i>L. campanulata</i> , <i>L. contaminata</i> (both varieties), <i>L. dehoopensis</i> , <i>L. esterhuysenae</i> , <i>L. hirta</i> (both varieties), <i>L. juncifolia</i> (both varieties), <i>L. mathewsii</i> , <i>L. moniliformis</i> , <i>L. montana</i> , <i>L. multifolia</i> , <i>L. namaquensis</i> , <i>L. orthopetala</i> , <i>L. patula</i> , <i>L. pearsonii</i> , <i>L. polyphylla</i> , <i>L. sargeantii</i> , <i>L. unifolia</i> (both varieties), <i>L. youngii</i> , <i>L. zeyheri</i> <i>P. corymbosa</i> , <i>P. paucifolia</i>

Although leaf shape is a product of length and width, the character provided additional group information in that species with short leaves, for example, were not necessarily restricted to particular leaf shapes, e.g. *L. pusilla* had short, lanceolate leaves whereas *L. arida* had short, linear leaves, similarly *L. alba* had long, lanceolate leaves and *L. mathewsii* had long linear leaves. This implies different genetic constraints potentially through different ancestry.

A high level of variation occurred within each of the basic lamina shapes, from narrowly to broadly ovate, as in *L. carnosa* and *L. trichophylla* subsp. *trichophylla*, and from narrowly to broadly lanceolate, as in *L. haarlemensis* and *L. aloides*, and from narrowly to broadly linear, as in *L. moniliformis* and *L. hirta* (Figure 11).



Lamina shape was stable within species and has diagnostic potential. Leaf shape did not appear to correlate to habitat type as both narrow- and broad-leaved species occurred in moist and arid environments.

The morphology of the distal and proximal areas of adult leaves varied, consequently these areas were scored as different characters:

7) **Distal lamina profile (transverse)**. Three states occurred: flat (=0); canaliculate (=1); and convex (=2). Qualitative character, scored as character 18 (Appendix 1).

The distal portion of the leaves of *Massonia* was flat. In *Lachenalia* and *Polyxena* this state occurred in 50 (42%) species (48 *Lachenalia*, two *Polyxena*). In 60 (50%) species (57 *Lachenalia*, three *Polyxena*) distal lamina shape was canaliculate (long and concave, resembling a channel). In 10 (8%) *Lachenalia* species distal lamina shape was convex (Table 13).

Table 13. Variation in distal lamina profile in <i>Lachenalia</i>, <i>Polyxena</i> and the outgroup <i>Massonia</i>	
Character State	Species
Flat	<i>L. alba</i> , <i>L. aloides</i> (all eight varieties), <i>L. ameliae</i> , <i>L. angelica</i> , <i>L. aurioliae</i> , <i>L. bulbifera</i> , <i>L. capensis</i> , <i>L. carnosa</i> , <i>L. cernua</i> , <i>L. comptonii</i> , <i>L. congesta</i> , <i>L. dasybotrya</i> , <i>L. doleritica</i> , <i>L. elegans</i> (all four varieties), <i>L. fasciculata</i> , <i>L. fistulosa</i> , <i>L. giessii</i> , <i>L. gillettii</i> , <i>L. kliprandensis</i> , <i>L. lactosa</i> , <i>L. leomontana</i> , <i>L. liliiflora</i> , <i>L. longibracteata</i> , <i>L. lutea</i> , <i>L. margaretae</i> , <i>L. marginata</i> (both subspecies), <i>L. marlothii</i> , <i>L. martinae</i> , <i>L. minima</i> , <i>L. nardouwensis</i> , <i>L. neilii</i> , <i>L. nervosa</i> , <i>L. orchioides</i> (both varieties), <i>L. peersii</i> , <i>L. polypodantha</i> , <i>L. purpureocaerulea</i> , <i>L. pusilla</i> , <i>L. pustulata</i> , <i>L. schelpei</i> , <i>L. splendida</i> , <i>L. stayneri</i> , <i>L. thomasiae</i> , <i>L. trichophylla</i> (both subspecies), <i>L. unicolor</i> , <i>L. urceolata</i> , <i>L. valeriae</i> , <i>L. variegata</i> , <i>L. wiesei</i> <i>P. ensifolia</i> , <i>P. maughanii</i> <i>Massonia</i>
Canaliculate	<i>L. algoensis</i> , <i>L. anguinea</i> , <i>L. arbutnotiae</i> , <i>L. arida</i> , <i>L. attenuata</i> , <i>L. bachmannii</i> , <i>L. barkeriana</i> , <i>L. bolusii</i> , <i>L. bowkeri</i> , <i>L. buchbergensis</i> , <i>L. campanulata</i> , <i>L. canaliculata</i> , <i>L. concordiana</i> , <i>L. convallarioides</i> , <i>L. dehoopensis</i> , <i>L. duncanii</i> , <i>L. framesii</i> , <i>L. glauca</i> , <i>L. glaucophylla</i> , <i>L. haarlemensis</i> , <i>L. hirta</i> (both varieties), <i>L. inconspicua</i> , <i>L. isopetala</i> , <i>L. karooica</i> , <i>L. klinghardtiana</i> , <i>L. komsbergensis</i> , <i>L. latimeriae</i> , <i>L. leipoldtii</i> , <i>L. macgregoriorum</i> , <i>L. maximiliani</i> , <i>L. mediana</i> (both varieties), <i>L. montana</i> , <i>L. muiirii</i> , <i>L. mutabilis</i> , <i>L. namibiensis</i> , <i>L. nordenstamii</i> , <i>L. nutans</i> , <i>L. obscura</i> , <i>L. orthopetala</i> , <i>L. pearsonii</i> , <i>L. perryae</i> , <i>L. physocaulos</i> , <i>L. reflexa</i> , <i>L. rosea</i> , <i>L. rubida</i> , <i>L. salteri</i> , <i>L. sargeantii</i> , <i>L. undulata</i> (both subspecies), <i>L. unifolia</i> (both varieties), <i>L. ventricosa</i> , <i>L. verticillata</i> , <i>L. violacea</i> , <i>L. viridiflora</i> , <i>L. whitehillensis</i> , <i>L. xerophila</i> , <i>L. youngii</i> , <i>L. zebrina</i> <i>P. corymbosa</i> , <i>P. longituba</i> , <i>P. paucifolia</i>
Convex	<i>L. contaminata</i> (both varieties), <i>L. esterhuysenae</i> , <i>L. juncifolia</i> (both varieties), <i>L. mathewsii</i> , <i>L. moniliformis</i> , <i>L. multifolia</i> , <i>L. namaquensis</i> , <i>L. patula</i> , <i>L. polyphylla</i> , <i>L. zeyheri</i>

8) **Basal lamina profile (transverse)**. Two states occur: flat (=0); and canaliculate (=1). Qualitative character, scored as character 19 (Appendix 1).

The basal parts of the leaves of *Massonia* were flat. In *Lachenalia* and *Polyxena* this state occurred in 18 (15%) species (16 *Lachenalia*, two *Polyxena*), and in 102 (85%) species (99 *Lachenalia*, three *Polyxena*) the state was canaliculate (Table 14).

Character State	Species
Flat	<i>L. ameliae</i> , <i>L. angelica</i> , <i>L. congesta</i> , <i>L. contaminata</i> (both varieties), <i>L. dasybotrya</i> , <i>L. fasciculata</i> , <i>L. kliprandensis</i> , <i>L. moniliformis</i> , <i>L. multifolia</i> , <i>L. nervosa</i> , <i>L. polyphylla</i> , <i>L. polypodantha</i> , <i>L. purpureocaerulea</i> , <i>L. pusilla</i> , <i>L. stayneri</i> , <i>L. trichophylla</i> (both subspecies) <i>P. ensifolia</i> , <i>P. maughanii</i> <i>Massonia</i>
Canaliculate	<i>L. alba</i> , <i>L. algoensis</i> , <i>L. aloides</i> (all eight varieties), <i>L. anguinea</i> , <i>L. arbutnotiae</i> , <i>L. arida</i> , <i>L. attenuata</i> , <i>L. aurioliae</i> , <i>L. bachmannii</i> , <i>L. barkeriana</i> , <i>L. bolusii</i> , <i>L. bowkeri</i> , <i>L. buchbergensis</i> , <i>L. bulbifera</i> , <i>L. campanulata</i> , <i>L. canaliculata</i> , <i>L. capensis</i> , <i>L. carmosa</i> , <i>L. cernua</i> , <i>L. comptonii</i> , <i>L. concordiana</i> , <i>L. convallarioides</i> , <i>L. dehoopensis</i> , <i>L. doleritica</i> , <i>L. duncanii</i> , <i>L. elegans</i> (all four varieties), <i>L. esterhuysenae</i> , <i>L. fistulosa</i> , <i>L. framesii</i> , <i>L. giessii</i> , <i>L. gillettii</i> , <i>L. glauca</i> , <i>L. glaucophylla</i> , <i>L. haarlemensis</i> , <i>L. hirta</i> (both varieties), <i>L. inconspicua</i> , <i>L. isopetala</i> , <i>L. juncifolia</i> (both varieties), <i>L. karooica</i> , <i>L. klinghardtiana</i> , <i>L. komsbergensis</i> , <i>L. lactosa</i> , <i>L. latimerae</i> , <i>L. leipoldtii</i> , <i>L. leomontana</i> , <i>L. liliiflora</i> , <i>L. longibracteata</i> , <i>L. lutea</i> , <i>L. macgregoriorum</i> , <i>L. margaretae</i> , <i>L. marginata</i> (both subspecies), <i>L. marlothii</i> , <i>L. martinae</i> , <i>L. mathewsii</i> , <i>L. maximiliani</i> , <i>L. mediana</i> (both varieties), <i>L. minima</i> , <i>L. montana</i> , <i>L. muirii</i> , <i>L. mutabilis</i> , <i>L. namaquensis</i> , <i>L. namibiensis</i> , <i>L. nardouwensis</i> , <i>L. neilii</i> , <i>L. nordenstamii</i> , <i>L. nutans</i> , <i>L. obscura</i> , <i>L. orchioides</i> (both varieties), <i>L. orthopetala</i> , <i>L. patula</i> , <i>L. pearsonii</i> , <i>L. peersii</i> , <i>L. perryae</i> , <i>L. physocaulos</i> , <i>L. pustulata</i> , <i>L. reflexa</i> , <i>L. rosea</i> , <i>L. rubida</i> , <i>L. salteri</i> , <i>L. sargeantii</i> , <i>L. schelpei</i> , <i>L. splendida</i> , <i>L. thomasiae</i> , <i>L. undulata</i> (both subspecies), <i>L. unicolor</i> , <i>L. unifolia</i> (both varieties), <i>L. urceolata</i> , <i>L. valeriae</i> , <i>L. variegata</i> , <i>L. ventricosa</i> , <i>L. verticillata</i> , <i>L. violacea</i> , <i>L. viridiflora</i> , <i>L. whitehillensis</i> , <i>L. wiesei</i> , <i>L. xerophila</i> , <i>L. youngii</i> , <i>L. zebrina</i> , <i>L. zeyheri</i> <i>P. corymbosa</i> , <i>P. longituba</i> , <i>P. paucifolia</i>

9) **Leaf margin shape.** Two states occurred: flat margins (=0); and crisped margins (=1). Qualitative character, scored as character 23 (Appendix 1).

Massonia had flat leaf margins. In *Lachenalia* and *Polyxena* this state occurred in 118 (85%) taxa (113 *Lachenalia*, all five *Polyxena*). Crisped leaf margins occurred in 21 (15%) *Lachenalia* taxa (Table 15).

Table 15. Variation in leaf margin shape in <i>Lachenalia</i>, <i>Polyxena</i> and the outgroup <i>Massonia</i>	
Character State	Taxa
Flat	<p><i>L. alba</i>, <i>L. algoensis</i>, <i>L. aloides</i> (all eight varieties), <i>L. ameliae</i>, <i>L. angelica</i>, <i>L. anguinea</i>, <i>L. arbuthnotiae</i>, <i>L. arida</i>, <i>L. attenuata</i>, <i>L. aurioliae</i>, <i>L. bachmannii</i>, <i>L. barkeriana</i>, <i>L. bowkeri</i>, <i>L. bulbifera</i>, <i>L. campanulata</i>, <i>L. canaliculata</i>, <i>L. capensis</i>, <i>L. carnosa</i>, <i>L. cernua</i>, <i>L. comptonii</i>, <i>L. concordiana</i>, <i>L. congesta</i>, <i>L. contaminata</i> (both varieties), <i>L. convallarioides</i>, <i>L. dasybotrya</i>, <i>L. dehoopensis</i>, <i>L. doleritica</i>, <i>L. elegans</i> (all four varieties), <i>L. esterhuysenae</i>, <i>L. fasciculata</i>, <i>L. fistulosa</i>, <i>L. giessii</i>, <i>L. gillettii</i>, <i>L. glauca</i>, <i>L. glaucophylla</i>, <i>L. haarlemensis</i>, <i>L. hirta</i> (both varieties), <i>L. inconspicua</i>, <i>L. juncifolia</i> (both varieties), <i>L. karooica</i>, <i>L. kliprandensis</i>, <i>L. lactosa</i>, <i>L. latimerae</i>, <i>L. leipoldtii</i>, <i>L. leomontana</i>, <i>L. liliiflora</i>, <i>L. longibracteata</i>, <i>L. lutea</i>, <i>L. macgregoriorum</i>, <i>L. margaretae</i>, <i>L. mathewsii</i>, <i>L. maximiliani</i>, <i>L. mediana</i> var. <i>mediana</i>, <i>L. minima</i>, <i>L. moniliformis</i>, <i>L. montana</i>, <i>L. muirii</i>, <i>L. multifolia</i>, <i>L. mutabilis</i>, <i>L. namaquensis</i>, <i>L. namibiensis</i>, <i>L. nardouwensis</i>, <i>L. neilii</i>, <i>L. nervosa</i>, <i>L. nordenstamii</i>, <i>L. nutans</i>, <i>L. obscura</i>, <i>L. orchioides</i> (both varieties), <i>L. orthopetala</i>, <i>L. patula</i>, <i>L. pearsonii</i>, <i>L. peersii</i>, <i>L. perryae</i>, <i>L. physocaulos</i>, <i>L. polyphylla</i>, <i>L. polypodantha</i>, <i>L. purpureocaerulea</i>, <i>L. pusilla</i>, <i>L. pustulata</i>, <i>L. rosea</i>, <i>L. rubida</i>, <i>L. salteri</i>, <i>L. sargeantii</i>, <i>L. schelpei</i>, <i>L. splendida</i>, <i>L. stayneri</i>, <i>L. thomasiae</i>, <i>L. trichophylla</i> (both subspecies), <i>L. undulata</i> subsp. <i>grandifolia</i>, <i>L. unicolor</i>, <i>L. unifolia</i> (both varieties), <i>L. urceolata</i>, <i>L. valeriae</i>, <i>L. viridiflora</i>, <i>L. whitehillensis</i>, <i>L. youngii</i>, <i>L. zeyheri</i> <i>P. corymbosa</i>, <i>P. ensifolia</i>, <i>P. longituba</i>, <i>P. maughanii</i>, <i>P. paucifolia</i> <i>Massonia</i></p>
Crisped	<p><i>L. bolusii</i>, <i>L. buchbergensis</i>, <i>L. duncanii</i>, <i>L. framesii</i>, <i>L. isopetala</i>, <i>L. klinghardiana</i>, <i>L. komsbergensis</i>, <i>L. marginata</i> (both subspecies), <i>L. marlothii</i>, <i>L. martinae</i>, <i>L. mediana</i> var. <i>rogersii</i>, <i>L. reflexa</i>, <i>L. undulata</i> subsp. <i>undulata</i>, <i>L. variegata</i>, <i>L. ventricosa</i>, <i>L. verticillata</i>, <i>L. violacea</i>, <i>L. wiesei</i>, <i>L. xerophila</i>, <i>L. zebrina</i></p>

Margin shape was phenotypically plastic as the crisped margin state was often much reduced or frequently lost in cultivated specimens.

10) **Leaf apex shape.** Two states occurred: naviculate apices (=0); and acute apices (=1). Qualitative character, scored as character 25 (Appendix 1).

Massonia had naviculate (boat-shaped) leaf apices, in which the margins tapered to each end. In *Lachenalia* and *Polyxena* this state occurred in 98 (82%) species (96 *Lachenalia*, two *Polyxena*) (Figure 12A-C). In 22 (18%) species (19 *Lachenalia*, three *Polyxena*) leaf apices were acute, terminating in a point (Figure 12D-F, Table 16).

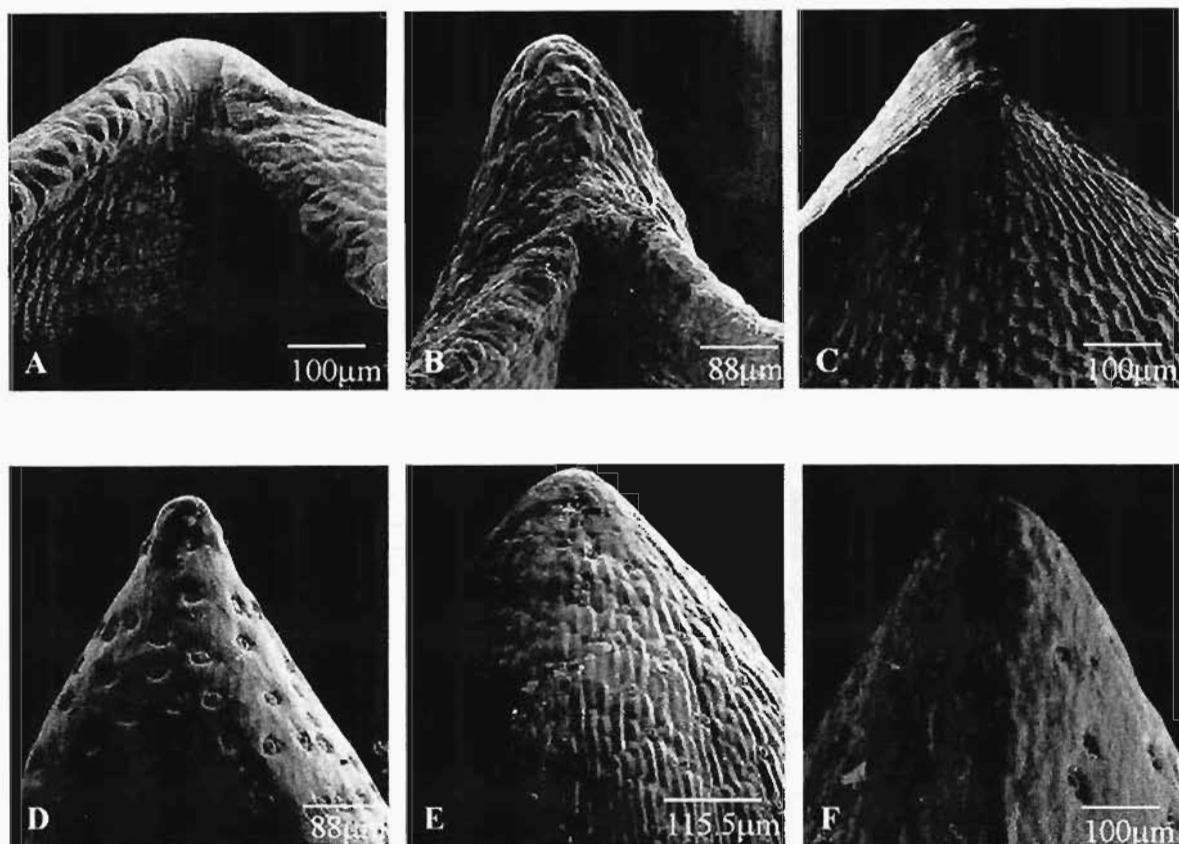


Figure 12. Scanning electron micrographs to illustrate variation in leaf apex shape in *Lachenalia* and *Polyxena*. Naviculate apices of A, *L. aloides* var. *vanzyliae* (Thomas s.n.); B, *L. martinae* (Duncan 141); C, *P. ensifolia* (Duncan 372). Acute apices of D, *L. polyphylla* (Duncan 348); E, *L. moniliformis* (Perry 795); F, *P. paucifolia* (Duncan 170).

Character State	Species
Naviculate	<i>L. alba</i> , <i>L. algoensis</i> , <i>L. aloides</i> (all eight varieties), <i>L. ameliae</i> , <i>L. angelica</i> , <i>L. arbuthnotiae</i> , <i>L. arida</i> , <i>L. attenuata</i> , <i>L. aurioliae</i> , <i>L. barkeriana</i> , <i>L. bolusii</i> , <i>L. bowkeri</i> , <i>L. buchbergensis</i> , <i>L. bulbifera</i> , <i>L. canaliculata</i> , <i>L. capensis</i> , <i>L. carnosae</i> , <i>L. cernua</i> , <i>L. comptonii</i> , <i>L. concordiana</i> , <i>L. congesta</i> , <i>L. dasybotrya</i> , <i>L. dehoopensis</i> , <i>L. doleritica</i> , <i>L. duncanii</i> , <i>L. elegans</i> (all four varieties), <i>L. fasciculata</i> , <i>L. fistulosa</i> , <i>L. framesii</i> , <i>L. giessii</i> , <i>L. gillettii</i> , <i>L. glauca</i> , <i>L. glaucophylla</i> , <i>L. haarlemensis</i> , <i>L. hirta</i> (both varieties), <i>L. inconspicua</i> , <i>L. isopetala</i> , <i>L. karooica</i> , <i>L. klinghardtiana</i> , <i>L. kliprandensis</i> , <i>L. komsbergensis</i> , <i>L. lactosa</i> , <i>L. latimerae</i> , <i>L. leipoldtii</i> , <i>L. leomontana</i> , <i>L. liliiflora</i> , <i>L. longibracteata</i> , <i>L. lutea</i> , <i>L. macgregoriorum</i> , <i>L. margaretae</i> , <i>L. marginata</i> (both subspecies), <i>L. marlothii</i> , <i>L. martinae</i> , <i>L. maximiliani</i> , <i>L. mediana</i> (both varieties), <i>minima</i> , <i>L. muirii</i> , <i>L. mutabilis</i> , <i>L. namibiensis</i> , <i>L. nardouwensis</i> , <i>L. neilii</i> , <i>L. nervosa</i> , <i>L. nordenstamii</i> , <i>L. nutans</i> , <i>L. obscura</i> , <i>L. orchioides</i> (both varieties), <i>L. pearsonii</i> , <i>L. peersii</i> , <i>L. perryae</i> , <i>L. physocaulos</i> , <i>L. polypodantha</i> , <i>L. purpureocaerulea</i> , <i>L. pusilla</i> , <i>L. pustulata</i> , <i>L. reflexa</i> , <i>L. rosea</i> , <i>L. rubida</i> , <i>L. salteri</i> , <i>L. schelpei</i> , <i>L. splendida</i> , <i>L. stayneri</i> , <i>L. thomasiae</i> , <i>L. trichophylla</i> (both subspecies), <i>L. undulata</i> (both subspecies), <i>L. unicolor</i> , <i>L. urceolata</i> , <i>L. valeriae</i> , <i>L. variegata</i> , <i>L. ventricosa</i> , <i>L. verticillata</i> , <i>L. violacea</i> , <i>L. viridiflora</i> , <i>L. whitehillensis</i> , <i>L. wiesei</i> , <i>L. xerophila</i> , <i>L. zebrina</i> <i>P. ensifolia</i> , <i>P. maughanii</i> <i>Massonia</i>
Acute	<i>L. anguinea</i> , <i>L. bachmannii</i> , <i>L. campanulata</i> , <i>L. contaminata</i> (both varieties), <i>L. convallarioides</i> , <i>L. esterhuysenae</i> , <i>L. juncifolia</i> (both varieties), <i>L. mathewsii</i> , <i>L. moniliformis</i> , <i>L. montana</i> , <i>L. multifolia</i> , <i>L. namaquensis</i> , <i>L. orthopetala</i> , <i>L. patula</i> , <i>L. polyphylla</i> , <i>L. sargeantii</i> , <i>L. unifolia</i> (both varieties), <i>L. youngii</i> , <i>L. zeyheri</i> <i>P. corymbosa</i> , <i>P. longituba</i> , <i>P. paucifolia</i>

5.7 SEED GERMINATION, JUVENILE LEAF MACROMORPHOLOGY AND ONTOGENY

Since families of monocotyledons are clearly characterised by their seedling type, the differentiation of these types must have happened early in monocot evolution. The development stage at which selective pressures would be expected to be maximal is that of early seedling development (Stebbins 1974). Some large families including Hyacinthaceae, have conservative seedling types even though they have undergone considerable adaptive radiation under widely different ecological conditions. Thus seedlings provide an important character set at family level. In many species germination only occurs under favourable conditions, therefore divergent radiation of vegetative characters is not strongly selected.

A consequence of this is that seedling structure frequently presents conservative character states that are useful in defining phylogenetic relationships (Tillich 2000).

Germination of the seeds in all *Lachenalia* and *Polyxena* species is hypogeal (Boyd 1932). The lower portion of the cotyledon consists of a short, tubular sheath, the hypophyll, and the upper portion consists of a very short, cylindrical stalk, the hyperphyll, which connects the cotyledon to the seed (Tillich 1995, 1998).

5.7.1 Materials and methods

Seeds of *Massonia*, all *Polyxena* and most *Lachenalia* species (except *L. doleritica*, *L. esterhuysenae*, *L. nordenstamii*, *L. nutans* and *L. sargeantii*) were gathered. The survey included as many population samples within variable species as possible, stored at room temperature and sown the following season under uniform conditions of growing medium, light intensity and irrigation frequency. Records of primary seedling leaf orientation and shape were made three months after germination.

5.7.2 Results

In *Massonia*, *Lachenalia* and *Polyxena*, a hypocotyl was not distinguishable on the cotyledon, but was included in the short cotyledonary sheath, so that the primary root appeared to be attached directly to the collar, at the base of the cotyledon (Figure 13). The length of the persistent primary root corresponded roughly to that of the aerial primary leaf length of the seedling. A ring of strong root hairs developed in the upper part of the primary root, just below the collar.

The lamina surfaces of first year seedlings were smooth in all species. Pustules and trichomes only developed during the second season of growth. The seeds of *Massonia* and all *Lachenalia* and *Polyxena* species took a single season of growth (roughly six months) from germination

to the formation of the first bulb.

Two seedling leaf characters were defined for the cladistic analyses:

1) **Primary seedling leaf orientation.** Three states occurred: prostrate (=0); suberect (=1); and erect leaves (=2). Quantitative character, scored as character 26 (Appendix 1).

Massonia had prostrate primary seedling leaves. In the 134 ingroup taxa investigated, 55 (41%) taxa (53 *Lachenalia*, two *Polyxena*) had prostrate primary seedling leaves (Figure 13A). In seven (5 %) *Lachenalia* taxa seedling leaves were suberect (angle of 50-70 degrees from the ground) (Figure 13B), and in 72 (54%) taxa (69 *Lachenalia*, three *Polyxena*) they were erect (angle of 85-90 degrees from the ground) (Figures 13C, 14, Table 17). The three basic types did not appear to correlate to particular habitat types, but the progressively flatter leaves did correlate with a progressive increase in lamina width. Prostrate primary seedling leaves frequently contained high levels of magenta anthocyanins in the upper mesophyll, resulting in brownish colouring of the adaxial surface. The orientation of the primary seedling leaf is stable within taxa, but sometimes deviates slightly or markedly from adult leaves (Table 18). Primary seedling leaf orientation was phenotypically plastic as the prostrate leaf state frequently became spreading or suberect where insufficiently high light levels existed under cultivation.

2) **Primary seedling leaf shape.** Two states occurred: flat leaves (=0); and terete leaves (=1). Qualitative character, scored as character 27 (Appendix 1).

Massonia had flat seedling leaves. In the 134 ingroup taxa investigated, 79 (59%) taxa (76 *Lachenalia*, three *Polyxena*) had terete seedling leaves, and 55 (41%) taxa (53 *Lachenalia*, two *Polyxena*) had flat seedling leaves. Terete seedling leaves had erect or suberect orientation and flat seedling leaves were always prostrate (Table 17).

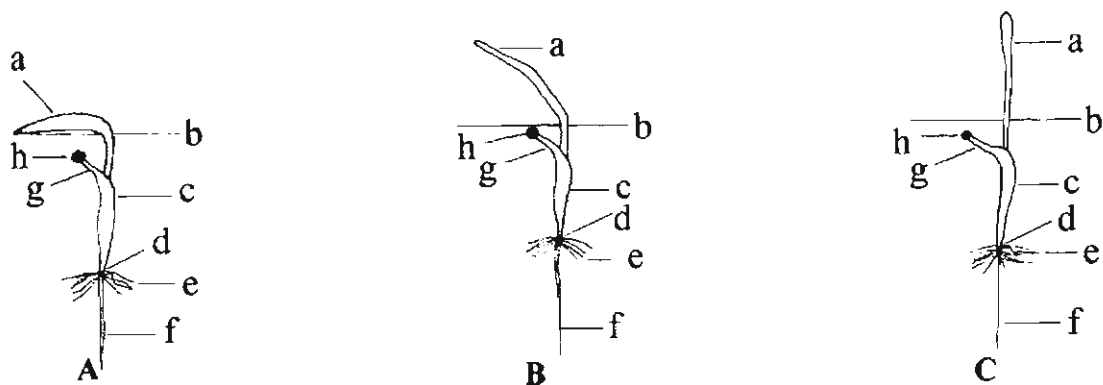


Figure 13. Variation in primary seedling leaf orientation and shape in *Lachenalia*.

A, prostrate, flat leaf of *L. peersii* (Duncan 280) X1;

B, suberect, terete leaf of *L. valeriae* (Duncan 444) X1;

C, erect, terete leaf of *L. mathewsii* (Duncan 200) X1.

a = primary leaf; b = ground level; c = cotyledonary

sheath (hypophyll); d = collar; e = root hairs; f = primary root;

g = cotyledonary stalk (hyperphyll); h = seed endosperm.

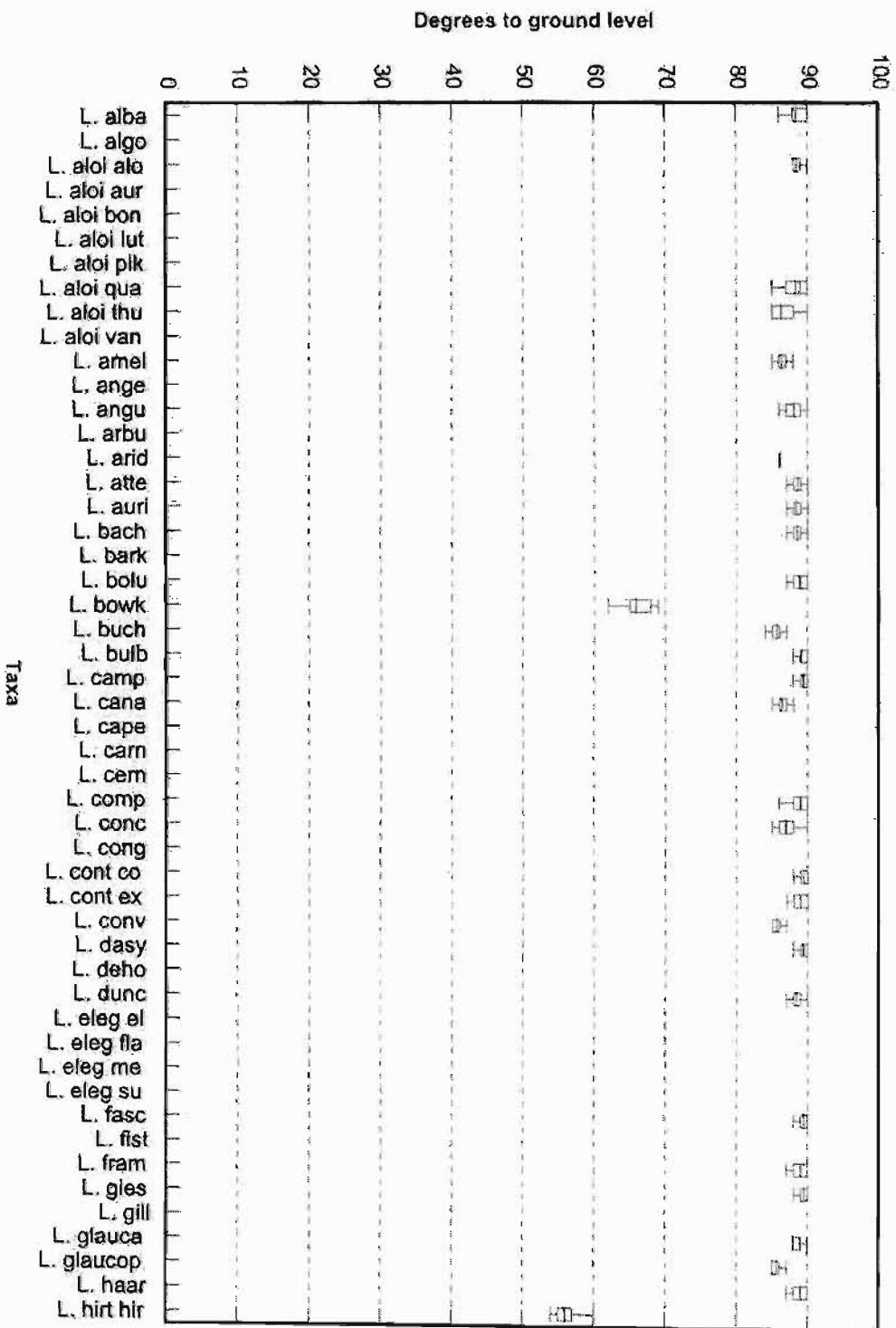


Figure 14. Seedling leaf orientation in Lachenalia and Polyxena

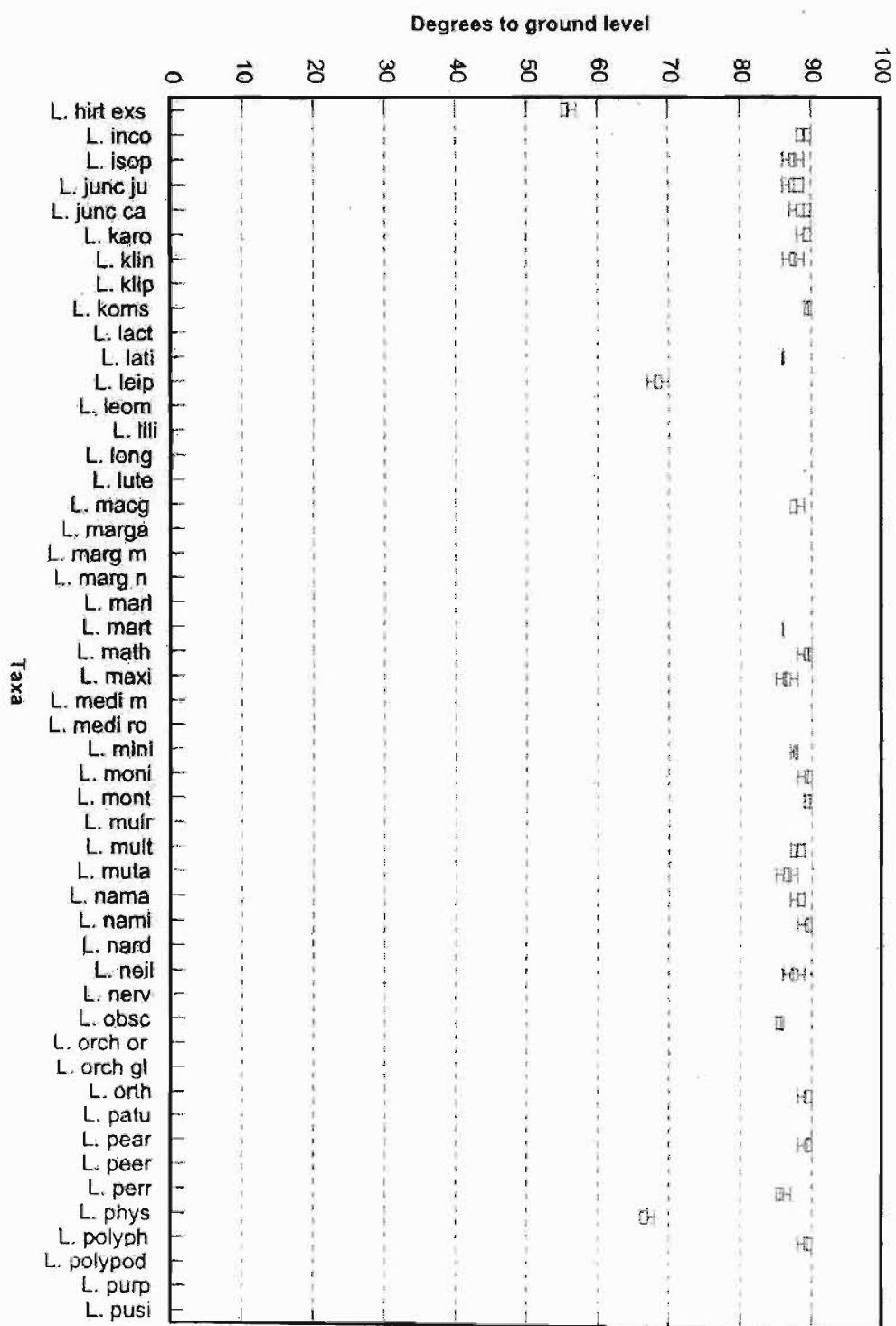


Figure 14. Seedling leaf orientation in Lachenalia and Polyxena

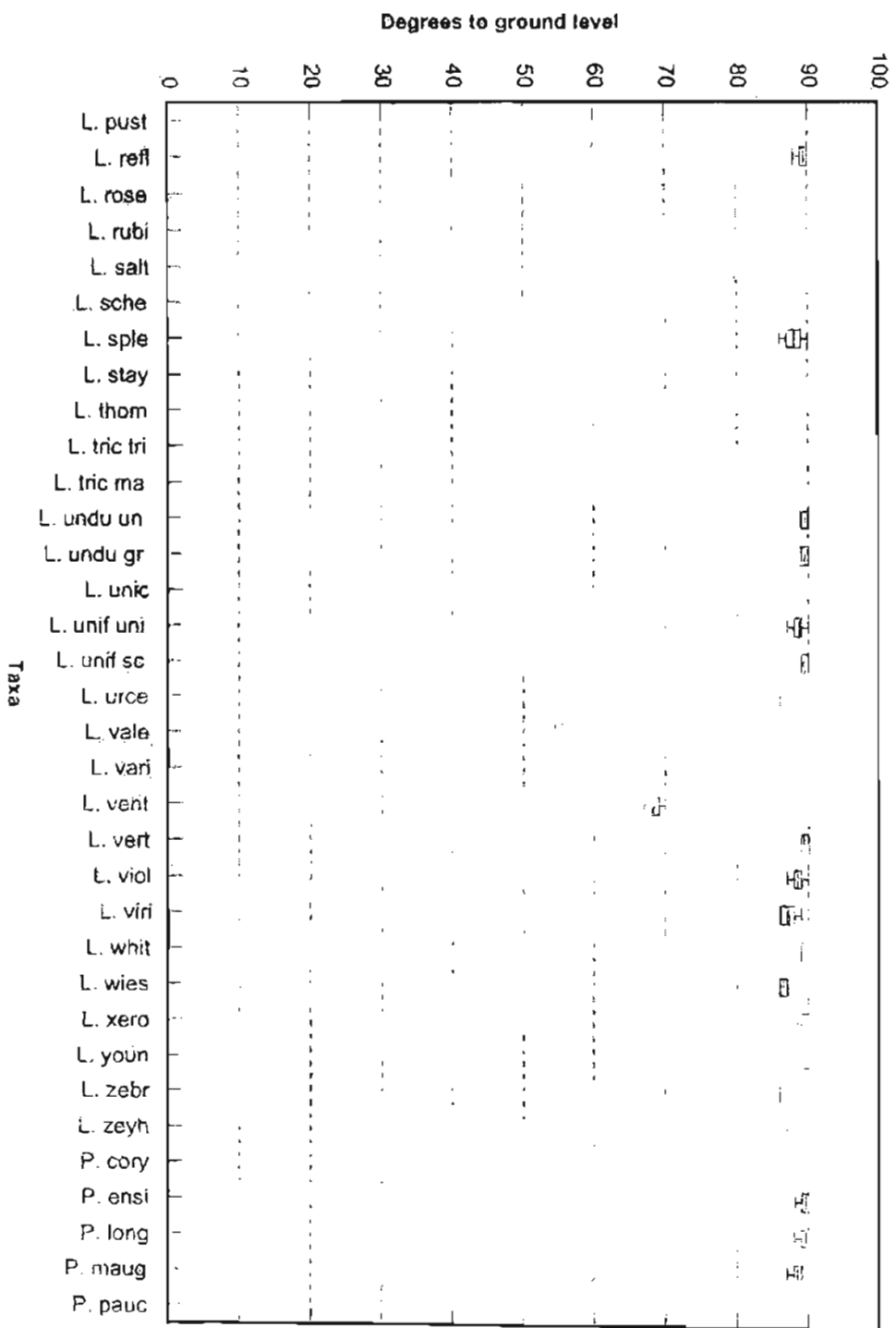


Figure 14. Seedling leaf orientation in Lachenalia and Polyxena

Table 17. Variation in primary seedling leaf orientation and shape in *Lachenalia*, *Polyxena* and the outgroup *Massonia*

Character State	Taxa
Prostrate and Flat	<p><i>L. algoensis</i>, <i>L. aloides</i> var. <i>aurea</i>, <i>L. aloides</i> var. <i>bonaspei</i>, <i>L. aloides</i> var. <i>luteola</i>, <i>L. aloides</i> var. <i>piketbergensis</i>, <i>L. aloides</i> var. <i>vanzyliae</i>, <i>L. angelica</i>, <i>L. arbuthnotiae</i>, <i>L. barkeriana</i>, <i>L. capensis</i>, <i>L. carnosae</i>, <i>L. cernua</i>, <i>L. congesta</i>, <i>L. dehoopensis</i>, <i>L. elegans</i> (all four varieties), <i>L. fistulosa</i>, <i>L. gillettii</i>, <i>L. kliprandensis</i>, <i>L. lactosa</i>, <i>L. leomontana</i>, <i>L. liliiflora</i>, <i>L. longibracteata</i>, <i>L. lutea</i>, <i>L. margaretae</i>, <i>L. marginata</i> (both subspecies), <i>L. marlothii</i>, <i>L. mediana</i> (both varieties), <i>L. muirii</i>, <i>L. nardouwensis</i>, <i>L. nervosa</i>, <i>L. orchioides</i> (both varieties), <i>L. patula</i>, <i>L. peersii</i>, <i>L. polypodantha</i>, <i>L. purpureocaerulea</i>, <i>L. pusilla</i>, <i>L. pustulata</i>, <i>L. rosea</i>, <i>L. rubida</i>, <i>L. salteri</i>, <i>L. schelpei</i>, <i>L. stayneri</i>, <i>L. thomasiae</i>, <i>L. trichophylla</i> (both subspecies), <i>L. unicolor</i>, <i>L. variegata</i> <i>P. corymbosa</i>, <i>P. paucifolia</i> <i>Massonia</i></p>
Suberect and Terete	<p><i>L. bowkeri</i>, <i>L. hirta</i> (both varieties), <i>L. leipoldtii</i>, <i>L. physocaulos</i>, <i>L. valeriae</i>, <i>L. ventricosa</i></p>
Erect and Terete	<p><i>L. alba</i>, <i>L. aloides</i> var. <i>aloides</i>, <i>L. aloides</i> var. <i>quadricolor</i>, <i>L. aloides</i> var. <i>thunbergii</i>, <i>L. ameliae</i>, <i>L. anguinea</i>, <i>L. arida</i>, <i>L. attenuata</i>, <i>L. aurioliae</i>, <i>L. bachmannii</i>, <i>L. bolusii</i>, <i>L. buchbergensis</i>, <i>L. bulbifera</i>, <i>L. campanulata</i>, <i>L. canaliculata</i>, <i>L. comptonii</i>, <i>L. concordiana</i>, <i>L. contaminata</i> (both varieties), <i>L. convallarioides</i>, <i>L. dasybotrya</i>, <i>L. duncanii</i>, <i>L. fasciculata</i>, <i>L. framesii</i>, <i>L. giessii</i>, <i>L. glauca</i>, <i>L. glaucophylla</i>, <i>L. haarlemensis</i>, <i>L. inconspicua</i>, <i>L. isopetala</i>, <i>L. juncifolia</i> (both varieties), <i>L. karoocica</i>, <i>L. klinghardtiana</i>, <i>L. komsbergensis</i>, <i>L. latimeriae</i>, <i>L. macgregoriorum</i>, <i>L. martinae</i>, <i>L. mathewsii</i>, <i>L. maximiliani</i>, <i>L. minima</i>, <i>L. moniliformis</i>, <i>L. montana</i>, <i>L. multifolia</i>, <i>L. mutabilis</i>, <i>L. namaquensis</i>, <i>L. namibiensis</i>, <i>L. neilii</i>, <i>L. obscura</i>, <i>L. orthopetala</i>, <i>L. pearsonii</i>, <i>L. perryae</i>, <i>L. polyphylla</i>, <i>L. reflexa</i>, <i>L. splendida</i>, <i>L. undulata</i> (both subspecies), <i>L. unifolia</i> (both varieties), <i>L. urceolata</i>, <i>L. verticillata</i>, <i>L. violacea</i>, <i>L. viridiflora</i>, <i>L. whitehillensis</i>, <i>L. wiesei</i>, <i>L. xerophila</i>, <i>L. youngii</i>, <i>L. zebrina</i>, <i>L. zeyheri</i> <i>P. ensifolia</i>, <i>P. longituba</i>, <i>P. maughanii</i></p>

Table 18. Deviation in primary seedling leaf and adult leaf orientation in *Lachenalia* and *Polyxena*

Character State	Taxa
Seedling leaves prostrate, adult leaves spreading to suberect	<i>L. algoensis</i> , <i>L. aloides</i> var. <i>aurea</i> , <i>L. aloides</i> var. <i>bonaspei</i> , <i>L. aloides</i> var. <i>luteola</i> , <i>L. aloides</i> var. <i>piketbergensis</i> , <i>L. aloides</i> var. <i>vanzyliae</i> , <i>L. arbutnotiae</i> , <i>L. barkeriana</i> , <i>L. capensis</i> , <i>L. carnosae</i> , <i>L. cernuae</i> , <i>L. dehoopensis</i> , <i>L. elegans</i> (all four varieties), <i>L. fistulosa</i> , <i>L. gillettii</i> , <i>L. lactosa</i> , <i>L. leomontana</i> , <i>L. liliiflora</i> , <i>L. longibracteata</i> , <i>L. lutea</i> , <i>L. margaretae</i> , <i>L. marginata</i> (both subspecies), <i>L. marlothii</i> , <i>L. mediana</i> (both varieties), <i>L. muirii</i> , <i>L. nardouwensis</i> , <i>L. orchioides</i> (both varieties), <i>L. peersii</i> , <i>L. polypodantha</i> , <i>L. purpureocaerulea</i> , <i>L. pustulata</i> , <i>L. rosea</i> , <i>L. rubida</i> , <i>L. salteri</i> , <i>L. schelpei</i> , <i>L. thomasiae</i> , <i>L. unicolor</i> , <i>L. variegata</i> <i>P. corymbosa</i> , <i>P. paucifolia</i>
Seedling leaves prostrate, adult leaves erect	<i>L. patula</i>
Seedling leaves erect, adult leaves spreading to suberect	<i>L. alba</i> , <i>L. aloides</i> var. <i>aloides</i> , <i>L. aloides</i> var. <i>quadricolor</i> , <i>L. aloides</i> var. <i>thunbergii</i> , <i>L. ameliae</i> , <i>L. anguinea</i> , <i>L. arida</i> , <i>L. attenuata</i> , <i>L. aurioliae</i> , <i>L. bachmannii</i> , <i>L. bolusii</i> , <i>L. buchbergensis</i> , <i>L. bulbifera</i> , <i>L. campanulata</i> , <i>L. canaliculata</i> , <i>L. comptonii</i> , <i>L. concordiana</i> , <i>L. convallarioides</i> , <i>L. dasybotrya</i> , <i>L. duncanii</i> , <i>L. fasciculata</i> , <i>L. framesii</i> , <i>L. giessii</i> , <i>L. glauca</i> , <i>L. glaucophylla</i> , <i>L. inconspicua</i> , <i>L. isopetala</i> , <i>L. juncifolia</i> (both varieties), <i>L. karooica</i> , <i>L. klinghardtiana</i> , <i>L. komsbergensis</i> , <i>L. latimeriae</i> , <i>L. macgregorium</i> , <i>L. martinae</i> , <i>L. mathewsii</i> , <i>L. maximiliani</i> , <i>L. minima</i> , <i>L. montana</i> , <i>L. mutabilis</i> , <i>L. namaquensis</i> , <i>L. namibiensis</i> , <i>L. neilii</i> , <i>L. obscura</i> , <i>L. orthopetala</i> , <i>L. pearsonii</i> , <i>L. perryae</i> , <i>L. reflexa</i> , <i>L. splendida</i> , <i>L. unifolia</i> (both varieties), <i>L. urceolata</i> , <i>L. verticillata</i> , <i>L. violacea</i> , <i>L. viridiflora</i> , <i>L. whitehillensis</i> , <i>L. wiesei</i> , <i>L. youngii</i> , <i>L. zebrina</i> , <i>L. zeyheri</i> <i>P. ensifolia</i> , <i>P. longituba</i> , <i>P. maughanii</i>

5.8 LEAF ANATOMY AND MICROMORPHOLOGY

According to Cutler (in Carter *et al.*, 1984), there are three orders of microsculpturing. These are primary sculpturing (cell shape), secondary sculpturing (topography of epidermal cell walls) and tertiary microsculpturing (finer topography superimposed on secondary sculpturing). Van Jaarsveld (1989) found sculpturing of the outer leaf epidermis to have high diagnostic value in distinguishing taxa in the genus *Gasteria* Duval, and Venter (1993) found it diagnostic for certain species in *Ledebouria* Roth. Epicuticular wax platelets were classified according to Barthlott *et al.* (1998).

Leaf margin micromorphology has been taxonomically useful in pointing out differences between species of *Gasteria* (Van Jaarsveld 1989) and *Kniphofia* (Codd 1968).

5.8.1 Materials and Methods

Electron Microscopy

Micromorphological studies were conducted on leaves harvested *in situ* and from the Kirstenbosch living collection. Specimens were collected and stored in 70% ethanol before dehydration in a graded series of ethanol. Tissue was cut into ca. 6 x 4 mm rectangular portions and critical point dried with liquid CO₂, after which it was mounted onto stubs with double-sided tape, and sputter-coated with gold-palladium. Samples were viewed using an Hitachi S-570 Scanning Electron Microscope (SEM), and a Philips XL 30 Environmental Scanning Electron Microscope (ESEM), at an acceleration voltage of 10 kV. Leaf samples were viewed roughly halfway between the base and apex of the leaf.

Anatomical studies were undertaken on material fixed in 50% F.A.A. (5 ml formaldehyde; 5 ml glacial acetic acid; 90 ml ethanol (50%)), dehydrated in a graded toluene series, embedded in wax and cut with a rotary microtome, set at 10 micrometers. Sections were mounted onto microscope slides using Haupt's Glue, then stained with alcian green-safranin, and examined by means of light microscopy.

For examination of leaf margin anatomy, hand-cut transverse sections of fresh leaf material of 112 *Lachenalia* species (including all subspecies and varieties) and all *Polyxena* species were made. Sections were placed onto microscope slides in water droplets, mounted with a cover slip, and either photographed using a Zeiss Photomicroscope, or sketched.

5.8.2 Results

5.8.2.1 Epidermis

Considerable primary, secondary and tertiary microsculpturing of the epidermis existed in *Lachenalia* and *Polyxena*. Epidermal cells occurred as a single layer in all species.

Vesture of the adaxial and abaxial lamina surfaces was diagnostic for several species. *L. ameliae* and *L. comptonii* had simple, multicellular trichomes restricted to the adaxial lamina. (Figure 16A, D, E). *L. hirta* var. *hirta* and *L. hirta* var. *exserta* had simple, multicellular trichomes restricted to the abaxial lamina (Figure 16B, C). *L. angelica*, *L. polypodantha*, *L. trichophylla* subsp. *trichophylla* and *L. trichophylla* subsp. *massonii* had stellate trichomes restricted to the adaxial lamina (Figure 16F-L).

The adaxial and abaxial lamina surfaces of all *Lachenalia* and *Polyxena* species were covered by a thin to dense covering of epicuticular wax platelets, which were all of the irregular type due to their irregular margins (Figure 15). They protruded more or less perpendicularly from the cell surfaces.

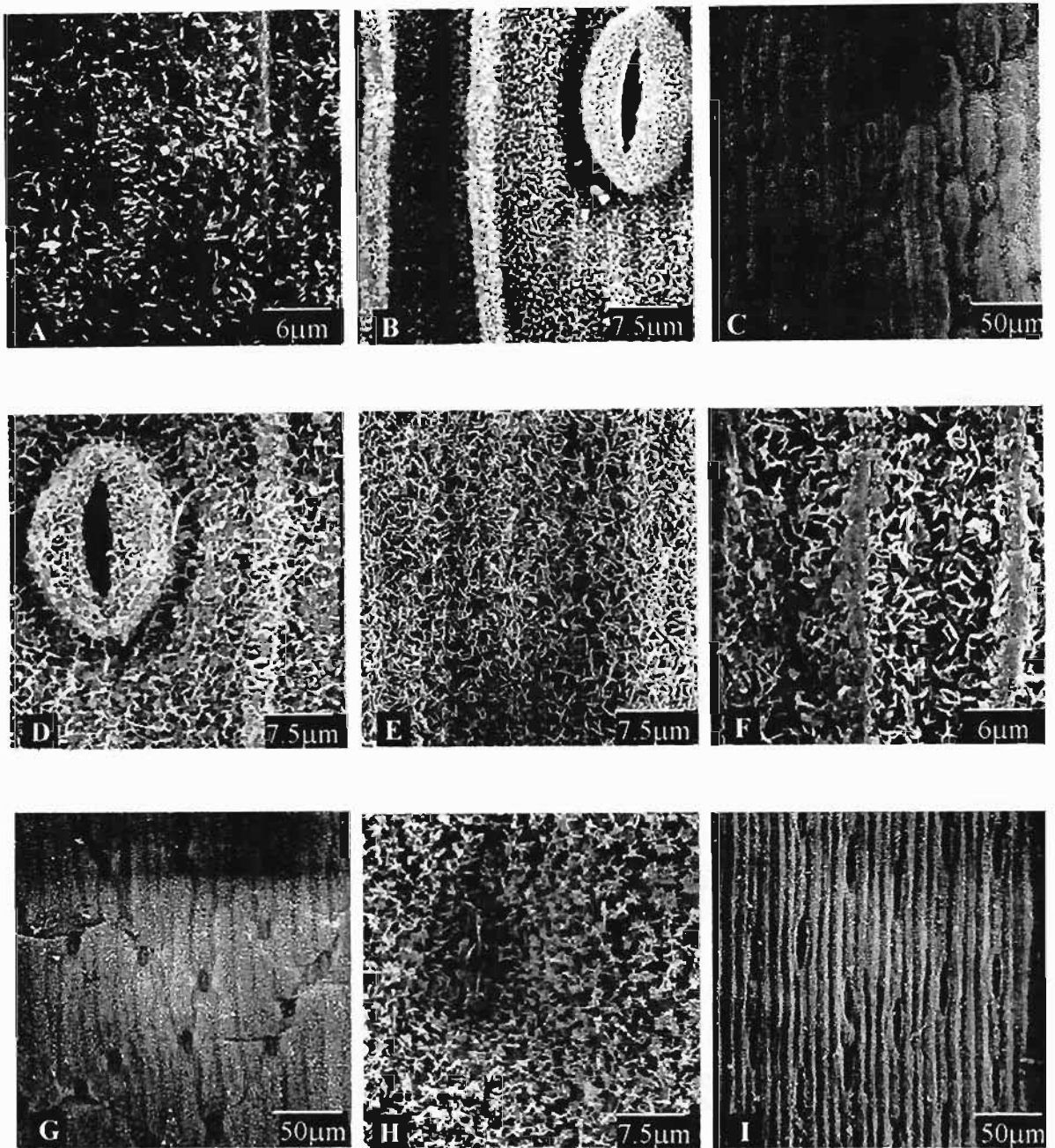


Figure 15. Scanning electron micrographs to illustrate variation in density of epicuticular wax platelets on lamina surfaces in *Lachenalia*.

Adaxial surfaces of A, *L. dehoopensis* (Scott s.n.); B, *L. longibracteata*

(Duncan 207); C, *L. aurioliae* (Duncan 394); D, *L. peersii* (Duncan 280);

E, *L. aloides* var. *luteola* (Duncan 89); F, *L. aloides* var. *quadricolor*

(Duncan 152); G, *L. isopetala* (Perry 3065).

Abaxial surfaces of H, *L. isopetala* (Perry 3065); I, *L. ventricosa* (Duncan 285).

The leaves of all *Lachenalia* and *Polyxena* species were amphistomatic and anomocytic. Stoma shape varied from almost round as in *L. dehoopensis* (Figure 17L), to narrowly elliptical as in *L. ventricosa* (Figure 15I), or elliptical as in *L. peersii* (Figure 15D). Most species had elliptical stomata. Stoma shape was usually consistent on the adaxial and abaxial surfaces, but in a few taxa stoma shape varied. *L. mutabilis* and *L. zeyheri* had elliptical stomata on the adaxial surface and narrowly elliptical stomata on the abaxial surface, and *L. dehoopensis* had almost round stomata on the adaxial surface and elliptical stomata on the abaxial surface. The level at which stomata were positioned varied from deep crypts as in *L. ventricosa* (Figure 15I), shallow crypts as in *L. lutea* (Figure 17H), or protruding as in *L. dehoopensis* (Figure 17L). The stomata of all *Polyxena* and most *Lachenalia* species occurred in shallow crypts. Four xeric species (*L. buchbergensis*, *L. multifolia*, *L. pearsonii* and *L. polypodantha*) had conspicuously few stomata on both the adaxial and abaxial surfaces. The stomata of three xerophytes (*L. isopetala*, *L. nordenstamii* and *L. zebrina*) and the mesophytic *L. ventricosa* were positioned in deep crypts, but generally stomatal position was not correlated to any particular habitat or leaf shape. Stoma shape and position were not found to form sufficiently distinct classes and were not used as characters in the cladistic analysis.

The cell walls of both the adaxial and abaxial lamina surfaces were papillate only in *L. bolusii*. The papillae were short and dome-shaped, and occurred singly or in longitudinal rows of one to seven papillae per cell. An interconnecting raised rim developed between each row of papillae (Figure 19 A,B), on page 81.

Two main types of epidermal cells occurred, namely elongate and fusiform epidermal cells (as seen in surface view), which were regular or irregular in shape and axially elongated. All *Polyxena* and most *Lachenalia* species had more or less elongate epidermal cells except for *L. leipoldtii*, *L. margaretae*, *L. patula* and *L. pusilla*, in which they were more or less fusiform (Figure 17D, G, I). Elongate epidermal cells varied in shape from relatively short and wide as in *L. stayneri* (Figure 17A), to long and narrow as in *L. mathewsii* (Figure

17B), and were mostly four-sided, with more or less straight walls. Elongate epidermal cells varied from 60-250 x 25-40 μm for the adaxial lamina, and from 160-250 x 15-50 μm for the abaxial lamina. Fusiform epidermal cells varied from long and narrow as in *L. pusilla* (Figure 17G), to extremely long and relatively wide as in *L. margaretae* (Figure 17D), and were mostly four-sided, with the walls distinctly tapering towards each end. Fusiform epidermal cell size varied from 300-350 x 15-30 μm , for both adaxial and abaxial surfaces. Primary epidermal cell sculpturing was not used as a character in the cladistic analyses as it did not form discontinuous states.

Species with prostrate leaves such as *L. angelica* and *L. stayneri* had the shortest adaxial epidermal cells but leaf shape did not appear to correlate to cell shape. In all species, the epidermal cells of the abaxial surfaces were as long as or much longer than those of the adaxial surfaces.

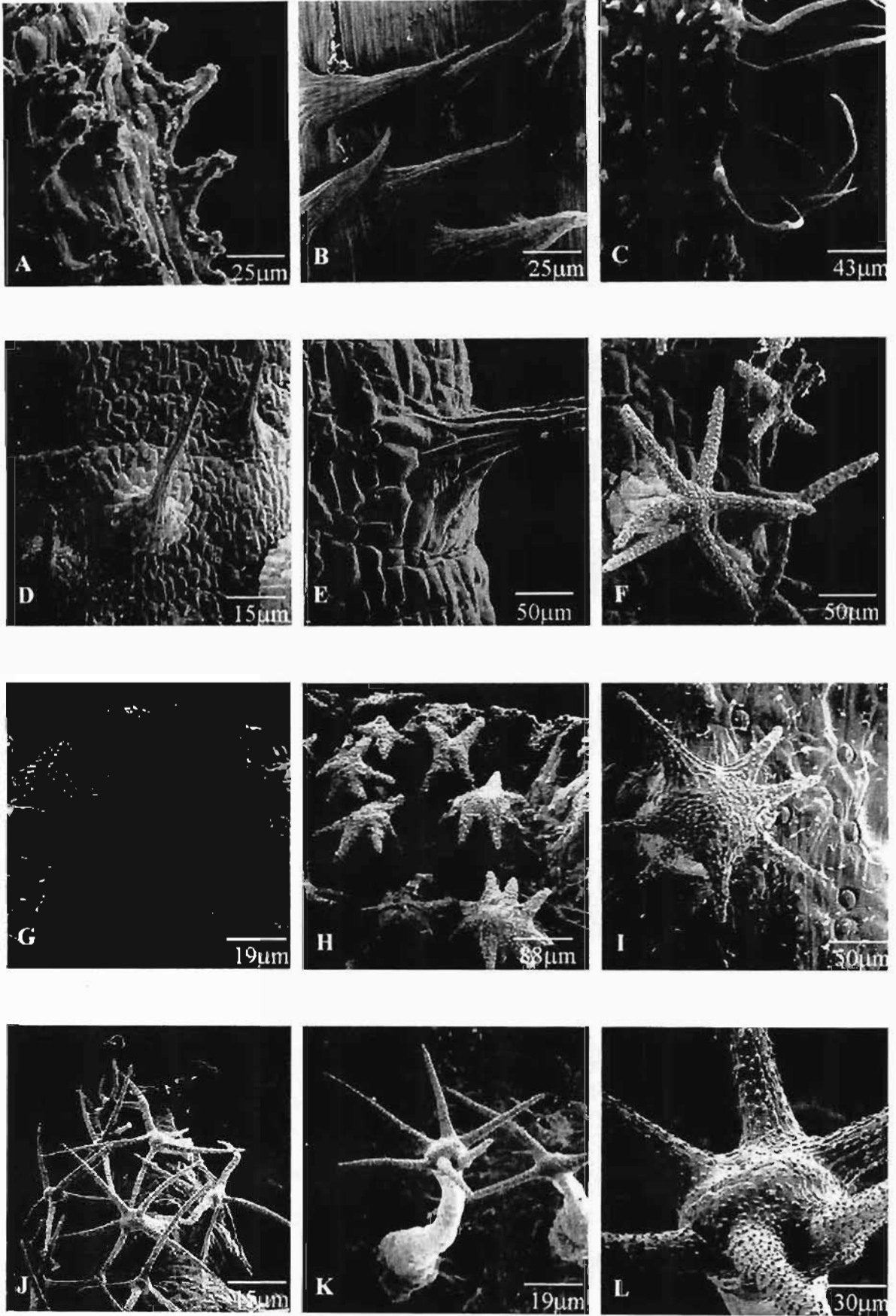
The secondary microsculpturing of the cell walls was variable. In surface in four *Lachenalia* taxa (*L. dehoopensis* (Figure 17L), *L. duncanii*, *L. trichophylla* subsp. *trichophylla* and *L. capensis*) it was almost flat, and in 27 taxa investigated (25 *Lachenalia*, two *Polyxena*) it was strongly convex (*L. arida*, *L. aurioliae*, *L. barkeriana*, *L. bulbifera* (Figure 17K), *L. carnososa*, *L. dasybotrya*, *L. framesii*, *L. glauca*, *L. inconspicua*, *L. isopetala*, *L. leipoldtii*, *L. macgregoriorum*, *L. margaretae*, *L. mathewsii*, *L. mediana* var. *mediana*, *L. mediana* var. *rogersii*, *L. namibiensis*, *L. nardouwensis*, *L. purpureocaerulea*, *L. splendida*, *L. valeriae*, *L. ventricosa*, *L. violacea*, *L. wiesei*, *L. zebrina*, *P. ensifolia* and *P. maughanii*). In *Massonia* and a further 100 taxa (97 *Lachenalia*, three *Polyxena*) secondary microsculpturing varied from slightly to medium convex. Secondary microsculpturing was not used as a character in the cladistic analyses as character states did not form sufficiently disjunct classes.

Three epidermal characters were defined for the cladistic analyses:

1) **Adaxial leaf trichomes.** Three states occurred: trichomes absent (=0); trichomes simple (=1); and trichomes stellate (=2). Qualitative character, scored as character 15 (Appendix 1).

Massonia lacked trichomes in common with 115 (96%) ingroup species (110 *Lachenalia*, all five *Polyxena*). Multicellular trichomes occurred in five *Lachenalia* species: in two (1.5%) species (*L. ameliae*, *L. comptonii*) simple trichomes occurred, and in three (2.5%) species (*L. angelica*, *L. polypodantha* and *L. trichophylla* (both subspecies)) trichomes were stellate.

The branches of stellate trichomes were unicellular or uniserial. The density and length of simple trichomes varied considerably within, and between, individuals of the same population. In *L. comptonii* (Figure 16D, E) trichomes ranged from 3-12 mm long, and in *L. ameliae* trichomes ranged from 1-5 mm long (Figure 16A). *L. hirta* var. *hirta* (Figure 16B, C) and *L. hirta* var. *exserta* were the only taxa with numerous stiff, multicellular trichomes restricted to the abaxial surface. These varied from 1.5-10.0 mm long (Figure 16B, C). In *L. ameliae*, the occurrence of trichomes varied within populations. Some individuals sported both long and short trichomes on their leaves, other individuals possessed only long trichomes. The stellate trichomes of *L. angelica*, *L. polypodantha* and *L. trichophylla* varied considerably in length (Figure 16F-L). The trichome stalks of the very short, stellate trichomes of *L. angelica* (Figure 16F, G) and *L. polypodantha* varied from 0.1-0.3 mm long, whereas those of *L. trichophylla* subsp. *trichophylla* varied from 0.3 -0.5 mm long (Figure 16H, I), and those of *L. trichophylla* subsp. *massonii* from 0.3 - 15.0 mm long (Figure 16J-L), depending on provenance. These characters were stable, expressing consistently *ex situ*. The stalks of the stellate trichomes of *L. trichophylla* subsp. *trichophylla* (which occurs in the southern parts of the distribution range of this species) were uniformly short, whereas those of *L. trichophylla* subsp. *massonii* (which occurs in the northern parts of the range) varied from short to very long on the same leaf (Barker 1980).



2) **Adaxial leaf tertiary sculpturing.** Six states occurred: finely striate (=0); laevigate (=1); median longitudinally ridged (=2); median longitudinally ridged and sides transversely ridged (=3); median finely striate and sides transversely ridged (=4); and transversely ridged (=5). Qualitative character, scored as character 20 (Appendix 1).

Massonia had finely striate cells and in the 135 taxa investigated, 29 (21%) *Lachenalia* taxa shared this character state (Figure 17 C). In 27 (20%) *Lachenalia* taxa the cells were laevigate (Figure 17A, B). In 44 (33%) taxa (42 *Lachenalia*, two *Polyxena*) the cell median was longitudinally ridged (Figure 17D-F). In 24 (18%) taxa (21 *Lachenalia*, three *Polyxena*) the cell median was longitudinally ridged and the sides were transversely ridged (Figure 17G-K). In three (2%) *Lachenalia* taxa the cell median was finely striate and the sides were transversely ridged, and in eight (6%) *Lachenalia* taxa the cells were transversely ridged (Figure 17L, Table 19).

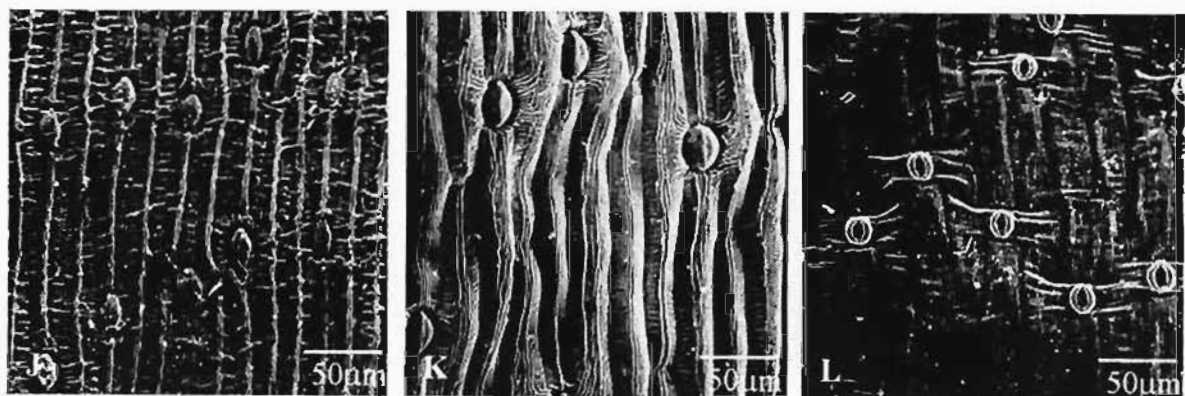
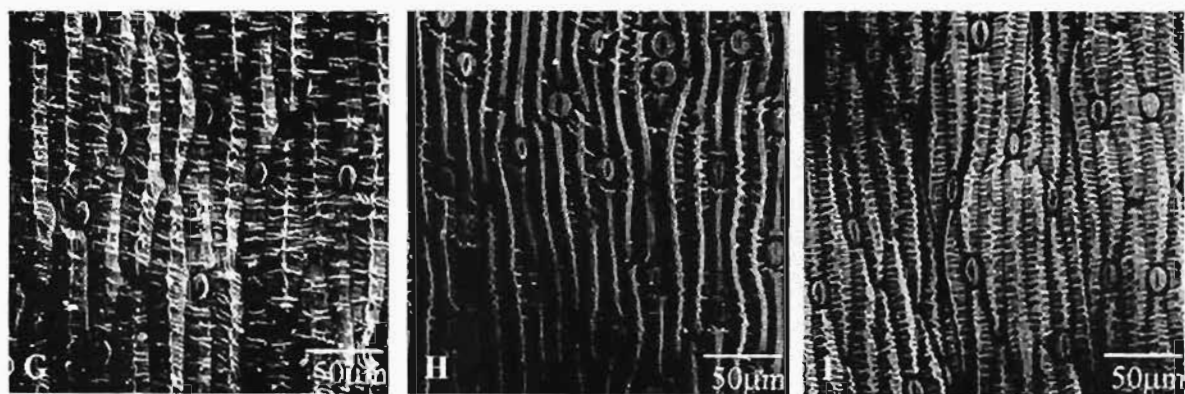
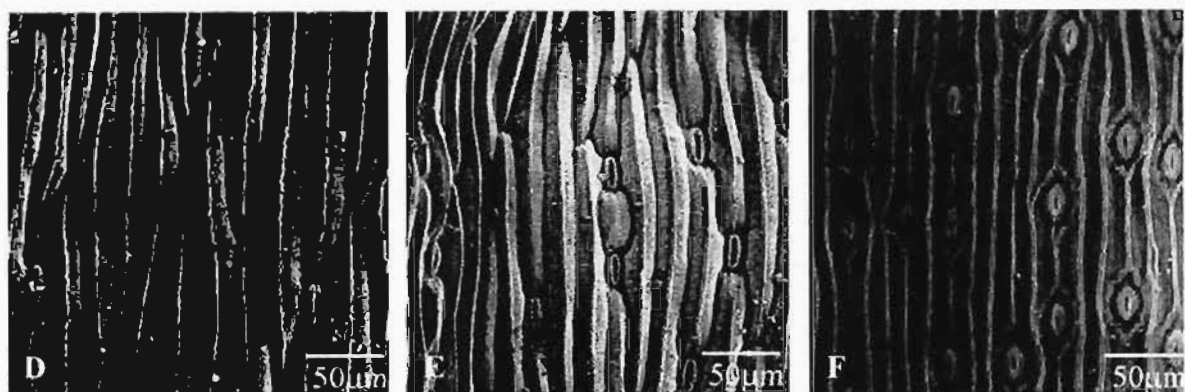
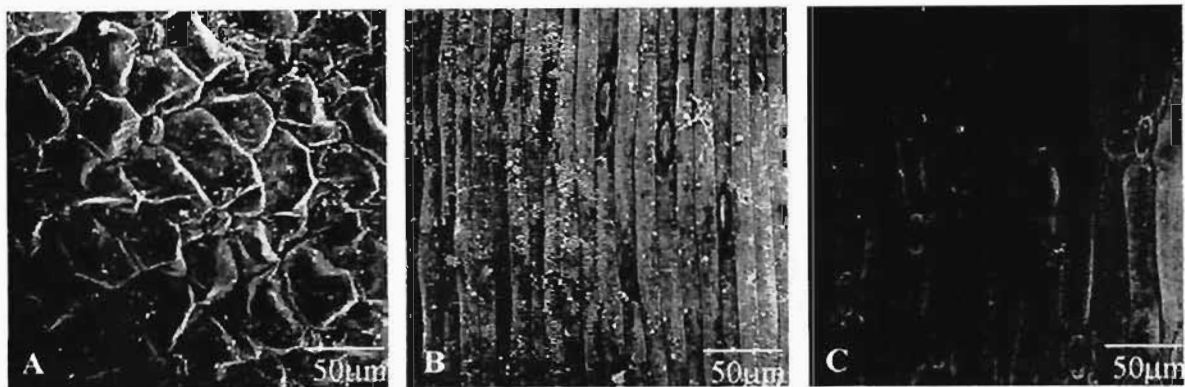


Table 19. Variation in adaxial leaf tertiary sculpturing in <i>Lachenalia</i>, <i>Polyxena</i> and the outgroup <i>Massonia</i>	
Character State	Taxa
Finely striate	<i>L. alba</i> , <i>L. ameliae</i> , <i>L. anguinea</i> , <i>L. attenuata</i> , <i>L. bachmannii</i> , <i>L. bowkeri</i> , <i>L. buchbergensis</i> , <i>L. fasciculata</i> , <i>L. hirta</i> var. <i>hirta</i> , <i>L. juncifolia</i> (both varieties), <i>L. latimerae</i> , <i>L. liliiflora</i> , <i>L. maximiliani</i> , <i>L. mediana</i> var. <i>rogersii</i> , <i>L. moniliformis</i> , <i>L. montana</i> , <i>L. multifolia</i> , <i>L. namaquensis</i> , <i>L. neilii</i> , <i>L. nordenslamii</i> , <i>L. purpureocaerulea</i> , <i>L. sargeantii</i> , <i>L. schelpei</i> , <i>L. thomasiae</i> , <i>L. undulata</i> subsp. <i>grandifolia</i> , <i>L. unifolia</i> (both varieties), <i>L. whitehillensis</i> <i>Massonia</i>
Laevigate	<i>L. angelica</i> , <i>L. aurioliae</i> , <i>L. bolusii</i> , <i>L. campanulata</i> , <i>L. comptonii</i> , <i>L. convallarioides</i> , <i>L. doleritica</i> , <i>L. duncanii</i> , <i>L. framesii</i> , <i>L. inconspicua</i> , <i>L. isopetala</i> , <i>L. karooica</i> , <i>L. lactosa</i> , <i>L. leomontana</i> , <i>L. longibracteata</i> , <i>L. martinae</i> , <i>L. mathewsii</i> , <i>L. nervosa</i> , <i>L. patula</i> , <i>L. polyphylla</i> , <i>L. reflexa</i> , <i>L. stayneri</i> , <i>L. trichophylla</i> (both subspecies), <i>L. viridiflora</i> , <i>L. zebrina</i> , <i>L. zeyheri</i>
Median longitudinally ridged	<i>L. algoensis</i> , <i>L. aloides</i> (all eight varieties), <i>L. arbutnotiae</i> , <i>L. barkeriana</i> , <i>L. canaliculata</i> , <i>L. contaminata</i> (both varieties), <i>L. glauca</i> , <i>L. haarlemensis</i> , <i>L. klinghardtiana</i> , <i>L. komsbergensis</i> , <i>L. macgregoriorum</i> , <i>L. margaretae</i> , <i>L. marginata</i> subsp. <i>marginata</i> , <i>L. mediana</i> var. <i>mediana</i> , <i>L. minima</i> , <i>L. muirii</i> , <i>L. mutabilis</i> , <i>L. obscura</i> , <i>L. orchioides</i> (both varieties), <i>L. orthopetala</i> , <i>L. peersii</i> , <i>L. perryae</i> , <i>L. physocaulos</i> , <i>L. rosea</i> , <i>L. rubida</i> , <i>L. salteri</i> , <i>L. urceolata</i> , <i>L. variegata</i> , <i>L. ventricosa</i> , <i>L. verticillata</i> , <i>L. violacea</i> , <i>L. wiesei</i> , <i>L. youngii</i> <i>P. maughanii</i> , <i>P. paucifolia</i>
Median longitudinally ridged, sides transversely ridged	<i>L. bulbifera</i> , <i>L. carnosae</i> , <i>L. cernua</i> , <i>L. dasybotrya</i> , <i>L. elegans</i> (all four varieties), <i>L. fistulosa</i> , <i>L. gillettii</i> , <i>L. glaucophylla</i> , <i>L. kliprandensis</i> , <i>L. leipoldtii</i> , <i>L. lutea</i> , <i>L. marginata</i> subsp. <i>neglecta</i> , <i>L. marlothii</i> , <i>L. nardouwensis</i> , <i>L. pusilla</i> , <i>L. pustulata</i> , <i>L. undulata</i> subsp. <i>undulata</i> , <i>L. unicolor</i> <i>P. corymbosa</i> , <i>P. ensifolia</i> , <i>P. longituba</i>
Median finely striate, sides transversely ridged	<i>L. congesta</i> , <i>L. namibiensis</i> , <i>L. splendida</i>
Transversely ridged	<i>L. arida</i> , <i>L. capensis</i> , <i>L. concordiana</i> , <i>L. dehoopensis</i> , <i>L. giessii</i> , <i>L. pearsonii</i> , <i>L. polypodantha</i> , <i>L. valeriae</i>

3) **Abaxial leaf tertiary sculpturing.** Four states occurred: finely striate (=0); laevigate (=1); median longitudinally ridged (=2); and transversely ridged (=3). Qualitative character, scored as character 21 (Appendix 1).

In *Massonia* these cells were finely striate. In the 135 ingroup taxa investigated, 37 (27%) taxa (35 *Lachenalia*, two *Polyxena*) had finely striate cells (Figure 18B-D). In 45 (33%) taxa (43 *Lachenalia*, two *Polyxena*) the cells were laevigate (Figure 18A). In 48 (36%) taxa (47 *Lachenalia* & *P. longituba*) the median was longitudinally ridged (Figure 18E-G), and in five (4%) *Lachenalia* taxa the cells were transversely ridged (Figures 18H, I, Table 20).

Character State	Taxa
Finely striate	<i>L. alba</i> , <i>L. anguinea</i> , <i>L. attenuata</i> , <i>L. buchbergensis</i> , <i>L. campanulata</i> , <i>L. canaliculata</i> , <i>L. carnososa</i> , <i>L. comptonii</i> , <i>L. congesta</i> , <i>L. contaminata</i> (both varieties), <i>L. dasybotrya</i> , <i>L. doleritica</i> , <i>L. fasciculata</i> , <i>L. hirta</i> var. <i>hirta</i> , <i>L. juncifolia</i> (both varieties), <i>L. kliprandensis</i> , <i>L. latimerae</i> , <i>L. maximiliani</i> , <i>L. moniliformis</i> , <i>L. montana</i> , <i>L. nardouwensis</i> , <i>L. neilii</i> , <i>L. obscura</i> , <i>L. orthopetala</i> , <i>L. purpureocaerulea</i> , <i>L. pustulata</i> , <i>L. sargeantii</i> , <i>L. schelpei</i> , <i>L. splendida</i> , <i>L. stayneri</i> , <i>L. undulata</i> subsp. <i>grandifolia</i> , <i>L. unicolor</i> , <i>L. zeyheri</i> <i>P. maughanii</i> , <i>P. paucifolia</i> <i>Massonia</i>
Laevigate	<i>L. aloides</i> (all eight varieties), <i>L. ameliae</i> , <i>L. arida</i> , <i>L. aurioliae</i> , <i>L. bachmannii</i> , <i>L. bulbifera</i> , <i>L. capensis</i> , <i>L. convallarioides</i> , <i>L. dehoopensis</i> , <i>L. duncanii</i> , <i>L. fistulosa</i> , <i>L. giessii</i> , <i>L. isopetala</i> , <i>L. karooica</i> , <i>L. klinghardtiana</i> , <i>L. leomontana</i> , <i>L. martinae</i> , <i>L. mathewsii</i> , <i>L. mediana</i> (both varieties), <i>L. minima</i> , <i>L. muirii</i> , <i>L. multifolia</i> , <i>L. nervosa</i> , <i>L. nordenstamii</i> , <i>L. patula</i> , <i>L. perryae</i> , <i>L. polyphylla</i> , <i>L. polypodantha</i> , <i>L. salteri</i> , <i>L. trichophylla</i> (both subspecies), <i>L. undulata</i> subsp. <i>undulata</i> , <i>L. unifolia</i> (both varieties), <i>L. youngii</i> <i>P. corymbosa</i> ; <i>P. ensifolia</i>
Median longitudinally ridged	<i>L. algoensis</i> , <i>L. arbutnotiae</i> , <i>L. barkeriana</i> , <i>L. cernua</i> , <i>L. concordiana</i> , <i>L. elegans</i> (all four varieties), <i>L. framesii</i> , <i>L. gillettii</i> , <i>L. glauca</i> , <i>L. haarlemensis</i> , <i>L. inconspicua</i> , <i>L. komsbergensis</i> , <i>L. leipoldtii</i> , <i>L. liliiflora</i> , <i>L. longibracteata</i> , <i>L. lutea</i> , <i>L. macgregoriorum</i> , <i>L. margaretae</i> , <i>L. marginata</i> (both subspecies), <i>L. marlothii</i> , <i>L. mutabilis</i> , <i>L. namaquensis</i> , <i>L. namibiensis</i> , <i>L. orchioides</i> (both varieties), <i>L. pearsonii</i> , <i>L. peersii</i> , <i>L. physocaulos</i> , <i>L. pusilla</i> , <i>L. reflexa</i> , <i>L. rosea</i> , <i>L. rubida</i> , <i>L. thomasiae</i> , <i>L. urceolata</i> , <i>L. valeriae</i> , <i>L. variegata</i> , <i>L. ventricosa</i> , <i>L. verticillata</i> , <i>L. violacea</i> , <i>L. viridiflora</i> , <i>L. whitehillensis</i> , <i>L. wiesei</i> , <i>L. zebrina</i> <i>P. longituba</i>
Transversely ridged	<i>L. angelica</i> , <i>L. bolusii</i> , <i>L. bowkeri</i> , <i>L. glaucophylla</i> , <i>L. lactosa</i>

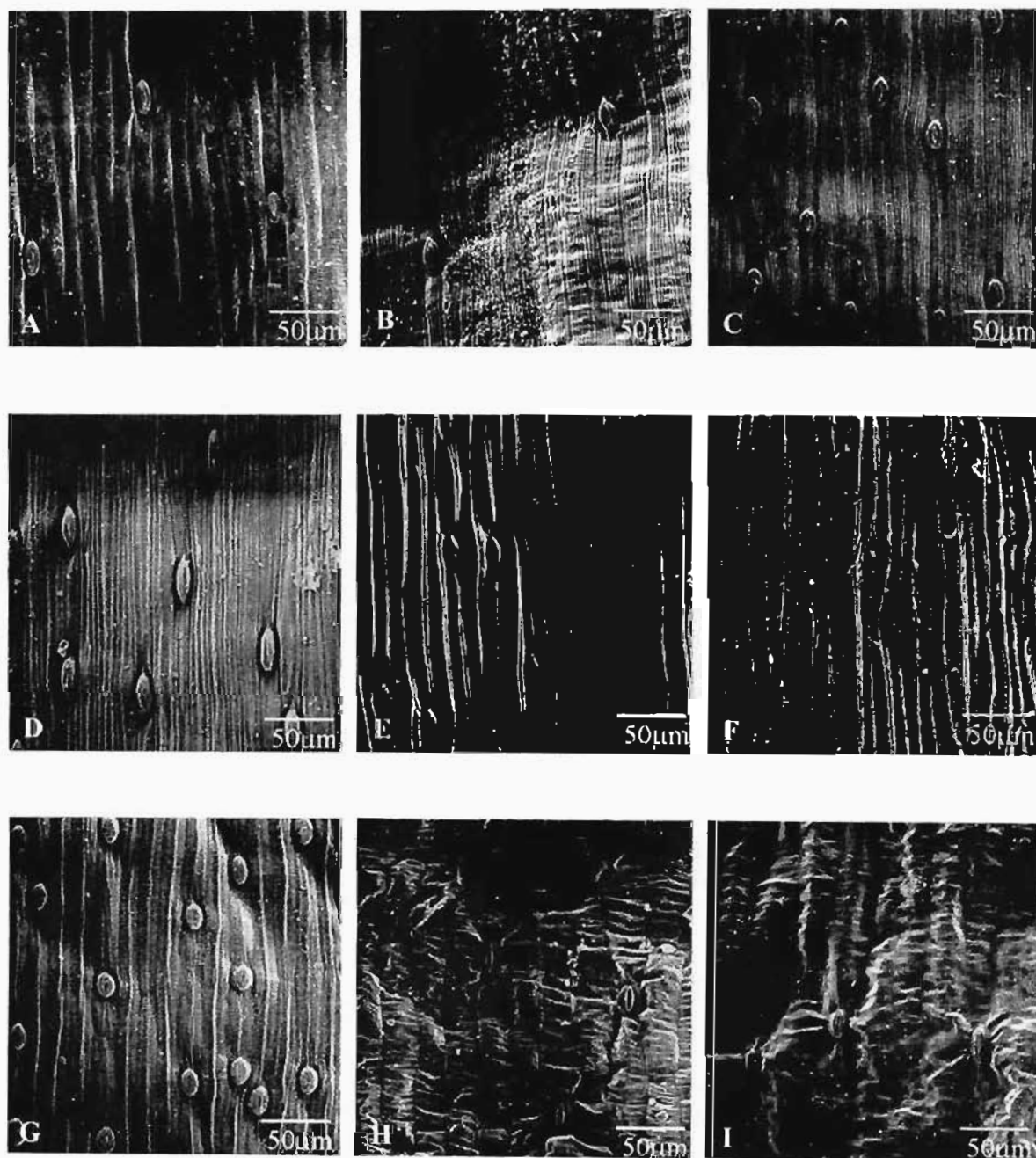


Figure 18. Scanning electron micrographs to illustrate variation in abaxial lamina tertiary sculpturing in *Lachenalia*. Laevigate cells of A, *L. fistulosa* (Duncan 452); finely striate cells of B, *L. pustulata* (Duncan 411); C, *L. maximiliani* (Duncan 284) and D, *L. orthopetala* (Duncan 262); cells with a longitudinally ridged median of E, *L. pusilla* (Duncan 210); F, *L. rubida* (Duncan 85) and G, *L. variegata* (Duncan 392); transversely ridged cells of H, *L. bolusii* (Duncan 256) and I, *L. angelica* (Duncan 244).

5.8.2.2 Mesophyll

The differences in the anatomy of the mesophyll tissue of leaves in *Lachenalia* and *Polyxena* in transverse section were mainly quantitative and of limited taxonomic use, and did not appear to correlate to leaf morphology, habitat or phytogeography.

Mesophyll anatomy of *Lachenalia* and *Polyxena* was placed into three broad types, but was not used in the cladistic analyses as it was unstable in eight *Lachenalia* species (*L. anguinea*, *L. glauca*, *L. klinghardtiana*, *L. namibiensis*, *L. obscura*, *L. orchioides*, *L. pustulata*, *L. splendida*), in which two of the three types occur, and in five *Lachenalia* species (*L. inconspicua*, *L. nordenstamii*, *L. physocaulos*, *L. schelpei*, *L. thomasiae*) adaxial cell shape layers were intermediate and graded into one another, and could not be accurately placed into particular types (Table 21).

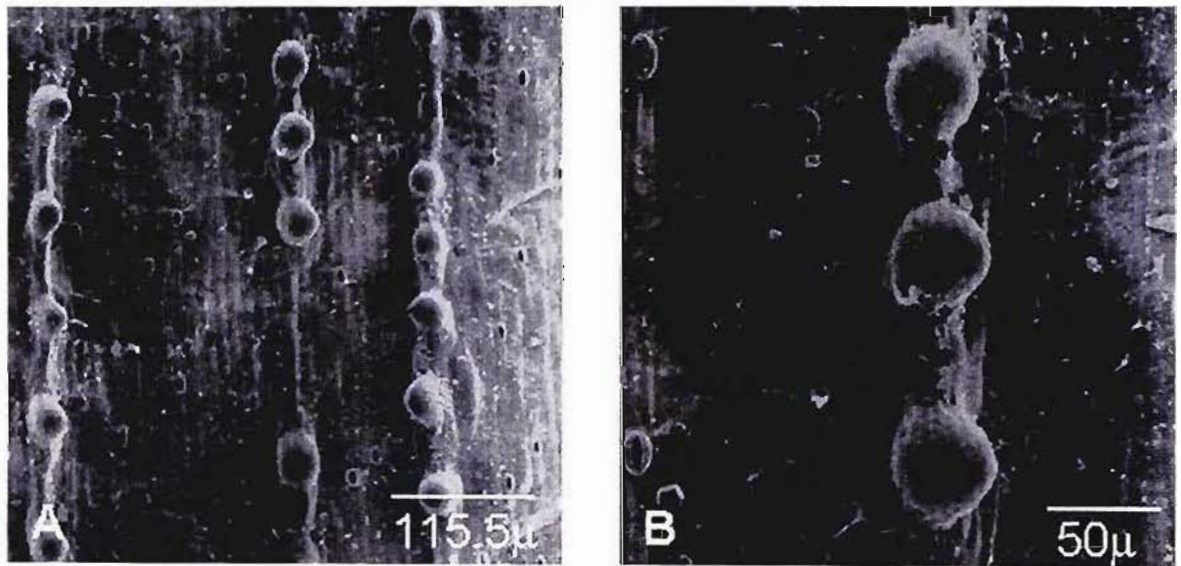


Figure 19. Scanning electron micrographs to illustrate adaxial lamina papillae in *L. bolusii* (Duncan256).

Table 21. Variation in mesophyll anatomy in <i>Lachenalia</i>, <i>Polyxena</i> and the outgroup <i>Massonia</i>	
Mesophyll cell layers	Species
2-5 layers adaxial chlorenchyma, 3-5 layers central spongy parenchyma, 2-3 layers abaxial chlorenchyma	<i>L. alba</i> , <i>L. angelica</i> , <i>L. anguinea</i> , <i>L. attenuata</i> , <i>L. aurioliae</i> , <i>L. bachmannii</i> , <i>L. buchbergensis</i> , <i>L. bulbifera</i> , <i>L. campanulata</i> , <i>L. canaliculata</i> , <i>L. capensis</i> , <i>L. cernua</i> , <i>L. concordiana</i> , <i>L. contaminata</i> (both varieties), <i>L. dehoopensis</i> , <i>L. duncanii</i> , <i>L. esterhuysenae</i> , <i>L. fasciculata</i> , <i>L. fistulosa</i> , <i>L. glauca</i> , <i>L. glaucophylla</i> , <i>L. hirta</i> (both varieties), <i>L. isopetala</i> , <i>L. juncifolia</i> (both varieties), <i>L. karooica</i> , <i>L. klinghardtiana</i> , <i>L. komsbergensis</i> , <i>L. lactosa</i> , <i>L. margaretae</i> , <i>L. martinae</i> , <i>L. mathewsii</i> , <i>L. maximiliani</i> , <i>L. mediana</i> (both varieties), <i>L. minima</i> , <i>L. moniliformis</i> , <i>L. montana</i> , <i>L. multifolia</i> , <i>L. mutabilis</i> , <i>L. namibiensis</i> , <i>L. neilii</i> , <i>L. obscura</i> , <i>L. orchioides</i> (both varieties), <i>L. pearsonii</i> , <i>L. perryae</i> , <i>L. polyphylla</i> , <i>L. pustulata</i> , <i>L. reflexa</i> , <i>L. rosea</i> , <i>L. rubida</i> , <i>L. sargeantii</i> , <i>L. splendida</i> , <i>L. trichophylla</i> (both subspecies), <i>L. urceolata</i> , <i>L. variegata</i> , <i>L. ventricosa</i> , <i>L. verticillata</i> , <i>L. violacea</i> , <i>L. whitehillensis</i> , <i>L. wiesei</i> , <i>L. youngii</i> , <i>L. zebrina</i> , <i>L. zeyheri</i> <i>P. corymbosa</i> , <i>P. longituba</i> , <i>P. paucifolia</i>
2-3 layers adaxial palisade chlorenchyma, 2-3 layers central spongy parenchyma, 2-3 layers abaxial chlorenchyma	<i>L. algoensis</i> , <i>L. aloides</i> (all eight varieties), <i>L. ameliae</i> , <i>L. anguinea</i> , <i>L. arbuthnotiae</i> , <i>L. arida</i> , <i>L. barkeriana</i> , <i>L. bolusii</i> , <i>L. carnosa</i> , <i>L. congesta</i> , <i>L. convallarioides</i> , <i>L. dasybotrya</i> , <i>L. doleritica</i> , <i>L. elegans</i> (all four varieties), <i>L. framesii</i> , <i>L. giessii</i> , <i>L. glauca</i> , <i>L. haarlemensis</i> , <i>L. klinghardtiana</i> , <i>L. kliprandensis</i> , <i>L. latimerae</i> , <i>L. leipoldtii</i> , <i>L. leomontana</i> , <i>L. longibracteata</i> , <i>L. lutea</i> , <i>L. macgregoriorum</i> , <i>L. marginata</i> (both subspecies), <i>L. marlothii</i> , <i>L. muirii</i> , <i>L. namaquensis</i> , <i>L. namibiensis</i> , <i>L. nardouwensis</i> , <i>L. nervosa</i> , <i>L. obscura</i> , <i>L. orchioides</i> (both varieties), <i>L. orthopetala</i> , <i>L. patula</i> , <i>L. peersii</i> , <i>L. polypodantha</i> , <i>L. purpureocaerulea</i> , <i>L. pusilla</i> , <i>L. pustulata</i> , <i>L. salteri</i> , <i>L. splendida</i> , <i>L. stayneri</i> , <i>L. thomasiae</i> , <i>L. undulata</i> (both subspecies), <i>L. unicolor</i> , <i>L. unifolia</i> (both varieties), <i>L. viridiflora</i> <i>P. ensifolia</i> , <i>P. maughanii</i> <i>Massonia</i>
1 layer adaxial chlorenchyma 2-3 layers adaxial palisade chlorenchyma, 2-3 layers central spongy parenchyma, 2-3 layers abaxial chlorenchyma	<i>L. bowkeri</i> , <i>L. comptonii</i> , <i>L. gillettii</i> , <i>L. liliiflora</i> , <i>L. valeriae</i>
adaxial cell shape layers intermediate 2-3 layers central spongy parenchyma, 2-3 layers abaxial chlorenchyma	<i>L. inconspicua</i> , <i>L. nordenstamii</i> , <i>L. physocaulos</i> , <i>L. schelpei</i> , <i>L. thomasiae</i>

Commonly, two to five layers of adaxial chlorenchyma, three to five layers of central spongy parenchyma and two to three layers of abaxial chlorenchyma occurred (Type one).

The second-most frequent type comprised two to three layers of adaxial palisade chlorenchyma, two to three layers of central spongy parenchyma, and two to three layers of abaxial chlorenchyma (Type two).

The least common type consisted of one layer of adaxial chlorenchyma, two to three layers of adaxial palisade chlorenchyma, two to three layers of central spongy parenchyma and two to three layers of abaxial chlorenchyma (Type three).

The adaxial and abaxial chlorenchymatous cells in Type one were generally about one third the size of the spongy parenchymatous cells, and sub-circular in transverse section. The adaxial palisade chlorenchyma cells in Type two and Type three were generally more than twice as long as they were broad. The spongy parenchyma cells were sub-circular in transverse section, and were either devoid of chloroplasts, or contained very few.

Raphides occurred in idioblasts of the mesophyll in all species of *Lachenalia* and *Polyxena*, primarily in the chlorenchyma.

Vascular bundles were arranged in a single row in transverse sections of all *Lachenalia* and *Polyxena* species, the xylem portion uppermost and the phloem beneath. Midvein bundle size was usually largest, with the remaining bundles either alternating with two to three small bundles between single large bundles for species with canaliculate or flat leaves (such as *L. macgregorium*, *P. ensifolia*), or with bundles more or less the same size in those species with subterete, linear leaves (such as *L. multifolia*, *P. corymbosa*). In all five *Polyxena* species prominent parenchymatous bundle sheaths were present but in *Lachenalia* this was variable, with prominent sheaths limited to *L. bowkeri* and *L. montana*. The highest number of vascular bundles counted in a lamina section was 42 bundles for *L. macgregorium*, and the lowest number was seven bundles for *L. multifolia*.

5.8.2.3 Leaf Margins

Two leaf margin characters were defined for the cladistic analyses:

1) **Leaf margin anatomy.** Five states occurred. Qualitative character, scored as character 22 (Appendix 1).

1. Simple margins, where the marginal cells were similar in size to the lamina epidermal cells in transverse section (=0); e.g. *L. montana* (Figure 20 A).

2. Flabellate margins (=1), which consisted of four subtypes;

2.1. vestigial flabellate margins, where the marginal cells were up to three times larger than the lamina epidermal cells in transverse section, and were arranged in a narrow fan around large central cells

2.2. ordinary flabellate margins, where similar marginal cells were arranged in a distinct fan in transverse section, e.g. *L. marginata* subsp. *marginata* (Figure 20 B)

2.3. elongate flabellate margins, where the central marginal cells were much longer than peripheral cells in transverse section

2.4. tapered flabellate margins, where all cells were very narrow in transverse section, tapering to a fine point, e.g. *L. salteri* (Figure 20 C).

3. 'Polyxena' margins, where a single additional marginal cell occurred in transverse section (=2), e.g. *P. ensifolia* (Figure 20 D).

4. Multi-epidermal margins, where three or four layers of marginal cells occurred in

transverse section (=3), e.g. *L. verticillata* (Figure 20 E).

5. Sclerotic margins, where three to five layers of marginal cells with hard, heavily lignified cell walls occurred in transverse section (=4), e.g. *L. duncanii* (Figure 20 F).

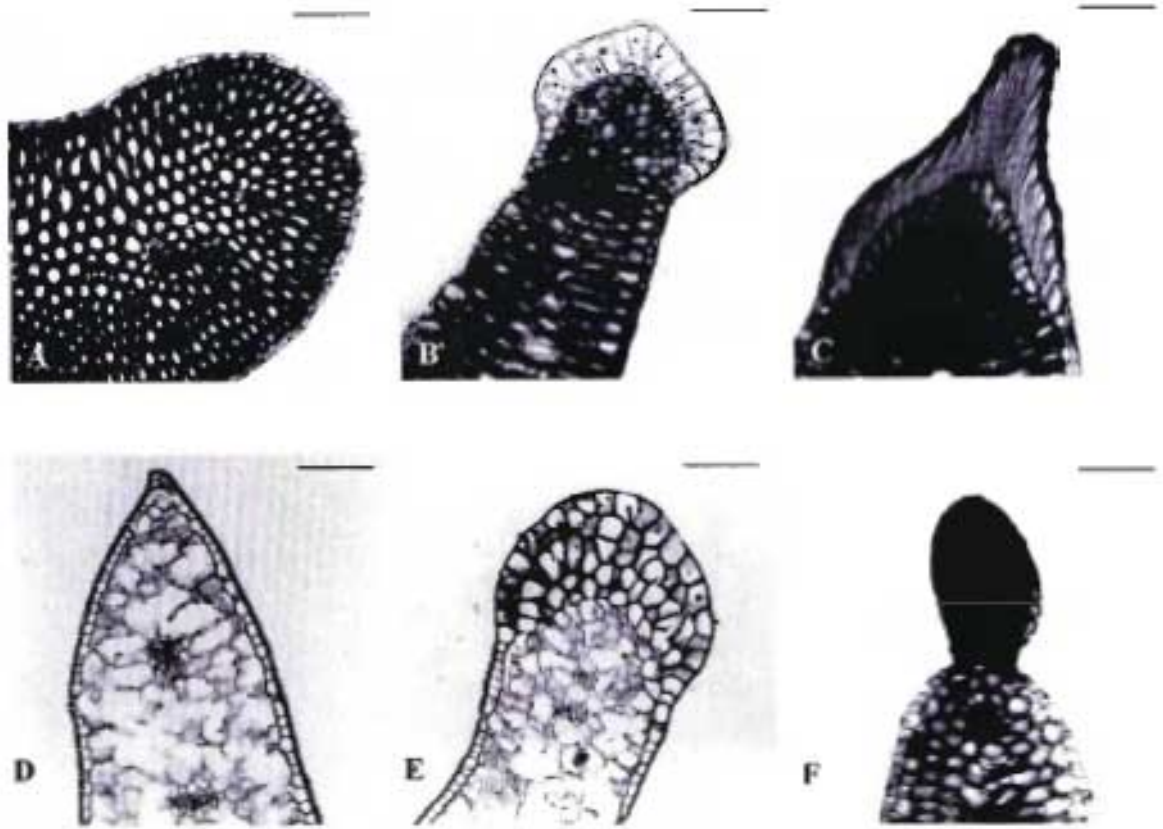


Figure 20. Variation in lamina margin anatomy in *Lachenalia* and *Polyxena*.

Transverse sections of A, simple margin of *L. montana* (Duncan 268);

B, ordinary flabellate margin of *L. marginata* subsp. *marginata* (Duncan 197);

C, tapered flabellate margin of *L. salteri* (Nicklin 136);

D, 'Polyxena' margin of *P. ensifolia* (Duncan 372);

E, multi-epidermal margin of *L. verticillata* (Müller-Doblies 88125);

F, sclerotic margin of *L. duncanii* (Duncan 189).

Scale bars = 150 μ m.

In *Massonia*, simple margins occurred. In the 117 *Lachenalia* and *Polyxena* species investigated, 58 (49%) *Lachenalia* species had flabellate margins, 36 (31%) species (33

Lachenalia, three *Polyxena*) had simple margins, 19 (16%) species (17 *Lachenalia*, two *Polyxena*) had 'Polyxena' margins, two (2 %) *Lachenalia* species had multiple epidermis margins, and two (2 %) *Lachenalia* species had sclerotic margins (Table 22).

Character state		Species
SIMPLE MARGIN		<i>L. ameliae</i> , <i>L. angelica</i> , <i>L. anguinea</i> , <i>L. barkeriana</i> , <i>L. bolusii</i> , <i>L. buchubergensis</i> , <i>L. comptonii</i> , <i>L. concordiana</i> , <i>L. contaminata</i> (both varieties), <i>L. convallarioides</i> , <i>L. framesii</i> , <i>L. glaucophylla</i> , <i>L. hirta</i> (both varieties), <i>L. juncifolia</i> (both varieties), <i>L. margaretae</i> , <i>L. mathewsii</i> , <i>L. maximiliani</i> , <i>L. moniliformis</i> , <i>L. montana</i> , <i>L. multifolia</i> , <i>L. namibiensis</i> , <i>L. nordenstamii</i> , <i>L. patula</i> , <i>L. pearsonii</i> , <i>L. polyphylla</i> , <i>L. polypodantha</i> , <i>L. sargeantii</i> , <i>L. thomasiae</i> , <i>L. trichophylla</i> (both subspecies), <i>L. unifolia</i> (both varieties), <i>L. urceolata</i> , <i>L. valeriae</i> , <i>L. zebrina</i> <i>P. corymbosa</i> , <i>P. longituba</i> , <i>P. paucifolia</i> <i>Massonia</i>
FLABELLATE MARGIN	Vestigial	<i>L. algoensis</i> , <i>L. aloides</i> (all eight varieties), <i>L. arbutnotiae</i> , <i>L. aurioliae</i> , <i>L. capensis</i> , <i>L. dehoopensis</i> , <i>L. doleritica</i> , <i>L. fasciculata</i> , <i>L. fistulosa</i> , <i>L. haarlemensis</i> , <i>L. karooica</i> , <i>L. klinghardtiana</i> , <i>L. lactosa</i> , <i>L. latimerae</i> , <i>L. leipoldtii</i> , <i>L. martiniae</i> , <i>L. mediana</i> (both varieties), <i>L. muirii</i> <i>L. mutabilis</i> , <i>L. peersii</i> , <i>L. perryae</i> , <i>L. physocaulos</i> , <i>L. pusilla</i> , <i>L. ventricosa</i> , <i>L. viridiflora</i> , <i>L. wiesei</i> , <i>L. youngii</i>
	Ordinary	<i>L. alba</i> , <i>L. bowkeri</i> , <i>L. elegans</i> (all four varieties), <i>L. longibracteata</i> , <i>L. lutea</i> , <i>L. marginata</i> (both subspecies), <i>L. marlothii</i> , <i>L. orchioides</i> (both varieties), <i>L. reflexa</i> , <i>L. variegata</i>
	Elongate	<i>L. canaliculata</i> , <i>L. cernua</i> , <i>L. gillettii</i> , <i>L. kliprandensis</i> , <i>L. leomontana</i> , <i>L. liliiflora</i> , <i>L. minima</i> , <i>L. obscura</i> , <i>L. purpureocaerulea</i> , <i>L. pustulata</i> , <i>L. rosea</i> , <i>L. schelpei</i> , <i>L. splendida</i> , <i>L. unicolor</i> , <i>L. violacea</i> , <i>L. whitehillensis</i>
	Tapered	<i>L. carnosa</i> , <i>L. glauca</i> , <i>L. inconspicua</i> , <i>L. nardouwensis</i> , <i>L. salteri</i>
'POLYXENA' MARGIN		<i>L. arida</i> , <i>L. attenuata</i> , <i>L. bachmannii</i> , <i>L. bulbifera</i> , <i>L. campanulata</i> , <i>L. congesta</i> , <i>L. dasybotrya</i> , <i>L. giessii</i> , <i>L. isopetala</i> , <i>L. komsbergensis</i> , <i>L. macgregoriorum</i> , <i>L. namaquensis</i> , <i>L. neilii</i> , <i>L. orthopetala</i> , <i>L. rubida</i> , <i>L. undulata</i> (both subspecies), <i>L. zeyheri</i> <i>P. ensifolia</i> , <i>P. maughanii</i>
MULTI-EPIDERMAL MARGIN		<i>L. stayneri</i> , <i>L. verticillata</i>
SCLEROTIC MARGIN		<i>L. duncanii</i> , <i>L. nervosa</i>

The sclerotic margins of *L. duncanii* and *L. nervosa* may deter edge-feeding invertebrate predators.

Leaf margin micromorphology corresponded to the five types of leaf margin anatomy and was not scored as a separate character (Table 23).

Character State	Species
Cell walls not thickened (=Simple margin)	<i>L. ameliae</i> , <i>L. angelica</i> , <i>L. anguinea</i> , <i>L. barkeriana</i> , <i>L. bolusii</i> , <i>L. buchubergensis</i> , <i>L. comptonii</i> , <i>L. concordiana</i> , <i>L. contaminata</i> (both varieties), <i>L. convallarioides</i> , <i>L. framesii</i> , <i>L. glaucophylla</i> , <i>L. hirta</i> (both varieties), <i>L. juncifolia</i> (both varieties), <i>L. margaretae</i> , <i>L. mathewsii</i> , <i>L. maximiliani</i> , <i>L. moniliformis</i> , <i>L. montana</i> , <i>L. multifolia</i> , <i>L. namibiensis</i> , <i>L. nordenstamii</i> , <i>L. patula</i> , <i>L. pearsonii</i> , <i>L. polyphylla</i> , <i>L. polypodantha</i> , <i>L. sargeantii</i> , <i>L. thomasiae</i> , <i>L. trichophylla</i> (both subspecies), <i>L. unifolia</i> (both varieties), <i>L. urceolata</i> , <i>L. valeriae</i> , <i>L. zebrina</i> <i>P. corymbosa</i> , <i>P. longituba</i> , <i>P. paucifolia</i> <i>Massonia</i>
Cell walls thickened, cells axially elongate (=Flabellate margin)	<i>L. alba</i> , <i>L. algoensis</i> , <i>L. aloides</i> (all eight varieties), <i>L. arbutnotiae</i> , <i>L. aurioliae</i> , <i>L. bowkeri</i> , <i>L. canaliculata</i> , <i>L. capensis</i> , <i>L. carnosa</i> , <i>L. cernua</i> , <i>L. dehoopensis</i> , <i>L. doleritica</i> , <i>L. elegans</i> (all four varieties), <i>L. fasciculata</i> , <i>L. fistulosa</i> , <i>L. gillettii</i> , <i>L. glauca</i> , <i>L. haarlemensis</i> , <i>L. inconspicua</i> , <i>L. karooica</i> , <i>L. klinghardtiana</i> , <i>L. kliprandensis</i> , <i>L. lactosa</i> , <i>L. latimerae</i> , <i>L. leipoldtii</i> , <i>L. leomontana</i> , <i>L. liliiflora</i> , <i>L. longibracteata</i> , <i>L. lutea</i> , <i>L. marginata</i> (both subspecies), <i>L. marlothii</i> , <i>L. martiniae</i> , <i>L. mediana</i> (both varieties), <i>L. minima</i> , <i>L. muiirii</i> , <i>L. perryae</i> , <i>L. physocaulos</i> , <i>L. purpureocaerulea</i> , <i>L. pusilla</i> , <i>L. pustulata</i> , <i>L. reflexa</i> , <i>L. rosea</i> , <i>L. salteri</i> , <i>L. schelpei</i> , <i>L. splendida</i> , <i>L. unicolor</i> , <i>L. variegata</i> , <i>L. ventricosa</i> , <i>L. violacea</i> , <i>L. viridiflora</i> , <i>L. whitehillensis</i> , <i>L. wiesei</i> , <i>L. youngii</i>
Cell walls not thickened, cells dome-shaped (='Polyxena' margin)	<i>L. arida</i> , <i>L. attenuata</i> , <i>L. bachmannii</i> , <i>L. bulbifera</i> , <i>L. campanulata</i> , <i>L. congesta</i> , <i>L. dasybotrya</i> , <i>L. giessii</i> , <i>L. isopetala</i> , <i>L. komsbergensis</i> , <i>L. macgregorium</i> , <i>L. namaquensis</i> , <i>L. neilii</i> , <i>L. orthopetala</i> , <i>L. rubida</i> , <i>L. undulata</i> (both subspecies), <i>L. zeyheri</i> <i>P. ensifolia</i> , <i>P. maughanii</i>
Cell walls thickened, cells isodiametric (=Multi-epidermal margin)	<i>L. stayneri</i> , <i>L. verticillata</i>
Cell walls heavily lignified, cells axially elongate (=Sclerotic margin)	<i>L. duncanii</i> , <i>L. nervosa</i>

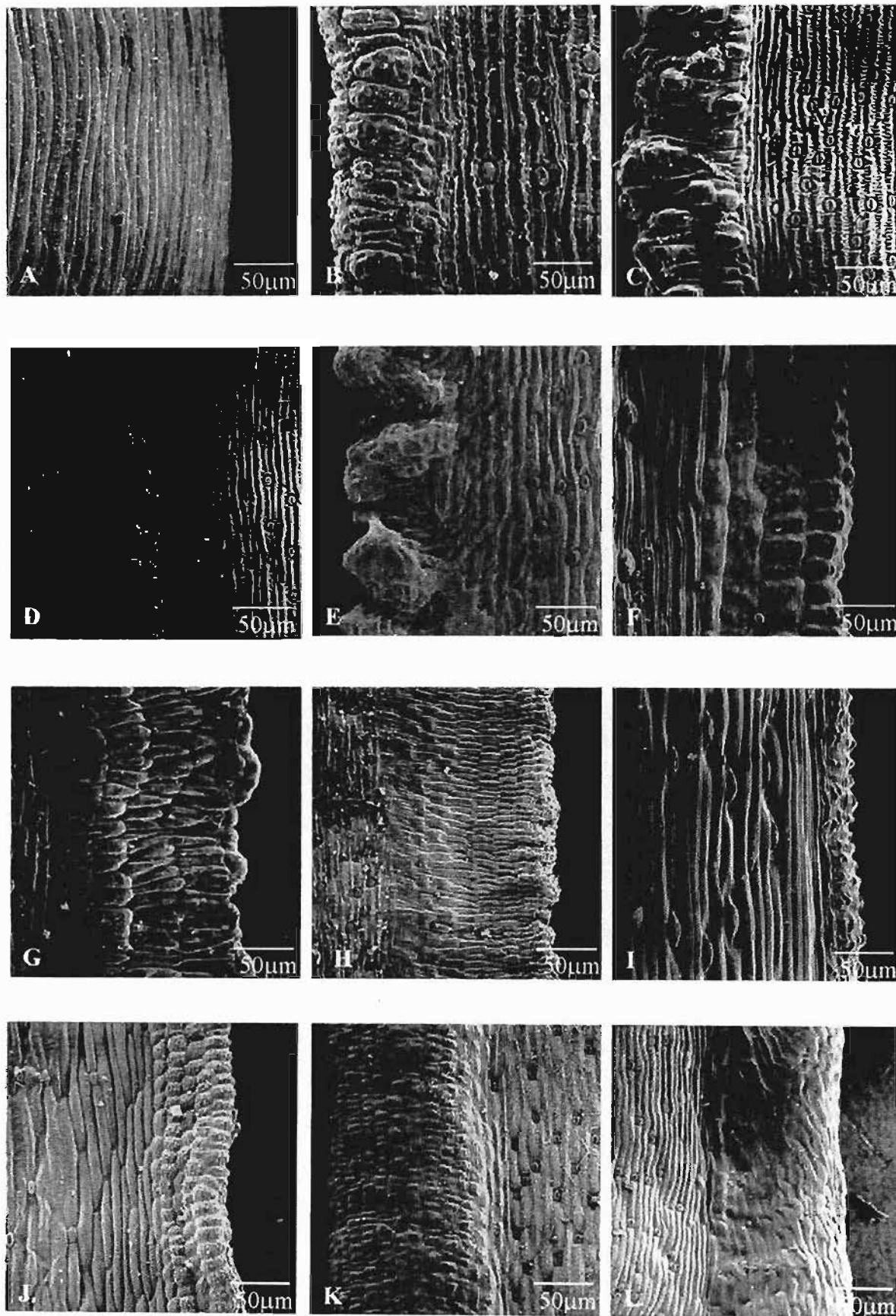
- 1) Simple margins, in which there was no epidermal cell wall thickening, e.g. *L. moniliformis* (Figure 21 A).
- 2) Flabellate margins, in which epidermal cell wall thickening occurred and the more or less fan-like arrangement of marginal cells resulted in axially elongate cells, e.g. vestigial flabellate margins of *L. arbutnotiae* and *L. leipoldtii* (Figure 21 B,C); ordinary flabellate

margins of *L. lutea* (Figure 21 D); elongate flabellate margins of *L. obscura*, *L. leomontana* and *L. rosea* (Figure 21 E,F,G); and tapered flabellate margins of *L. salteri* (Figure 21 H).

3) 'Polyxena' margins, in which there was no epidermal cell wall thickening and the single additional epidermal cell resulted in dome-shaped marginal cells e.g. *L. campanulata* (Figure 21 I).

4) Multi-epidermal margins, in which epidermal cell wall thickening occurred and the three to four layers of epidermal cells resulted in isodiametric cells e.g. *L. verticillata* (Figure 21 J).

5) Sclerotic margins, in which the heavily lignified cell walls resulted in axially elongate cells e.g. *L. nervosa* and *L. duncanii* (Figure 21 K,L).



Leaf margin type did not appear to correlate to leaf shape, habitat or phytogeography.

2) **Leaf margin vestiture.** Four states occurred: glabrous (=0); ciliolate (=1); ciliate (=2); and stellate margins (=3). Qualitative character, scored as character 24 (Appendix 1).

Glabrous margins occurred in *Massonia*, along with 107 (89%) ingroup species (105 *Lachenalia*, two *Polyxena*). In seven (6%) species the margins were ciliolate (*L. giessii*, *L. namibiensis*, *L. pearsonii*, *L. polyphylla*, *P. ensifolia*, *P. longituba* and *P. maughanii*). Three (2.5%) *Lachenalia* species had ciliate margins (*L. ameliae*, *L. comptonii* and *L. hirta*) (Figure 16A, C, E). Stellate trichomes were limited to the margins of three (2.5%) *Lachenalia* species (*L. angelica*, *L. polypodantha* and *L. trichophylla*) (Figure 16F-H, J).

5.9 INFLORESCENCE

Inflorescence initiation and development within the bulb occurs during the hot, dry summer (Roodbol & Niederwieser 1998).

5.9.1 Results

The inflorescences of *Lachenalia* and *Polyxena* were unbranched and axillary (Figures 22, 23). Potentially, a single inflorescence was produced annually per adult bulb in all species of *Lachenalia* and *Polyxena*. The orientation of inflorescences in all species of *Lachenalia* and *Polyxena* was erect to suberect, depending on degree of exposure to light. Most species had many-flowered inflorescences usually consisting of at least 15 flowers but certain taxa were usually few-flowered like *L. angelica* and *L. nordenstamii*, with fewer than 10 flowers. However, flower number was unstable and was strongly influenced by seasonal fluctuations in rainfall. Periods of excellent winter rainfall usually resulted in robust inflorescences with many more flowers than produced following moderate or low rainfall periods. No clearly discontinuous evolutionary classes were identified in flower number and the character was not

used in the cladistic analyses. The largest number of flowers counted on a single inflorescence was 73 for *L. anguinea*. Inflorescence length varied from 10 mm (*L. barkeriana*, *P. ensifolia*) to 300 mm (*L. anguinea*).

Two inflorescence characters were defined for the cladistic analyses:

1) Inflorescence type. Three states occurred: racemes (=0); spikes; (=1) and polymorphic (=2). Qualitative character, scored as character 36 (Appendix 1).

In *Massonia* the inflorescence was a corymbose or subcapitate raceme. In 102 (73%) ingroup taxa (97 *Lachenalia*, all five *Polyxena*), the inflorescence was a raceme, in which pedicel length varied from 0.5 mm up to 20 mm (Figure 22D-1). The racemes of two geoflorous, dwarf *Lachenalia* species were condensed into subcapitate inflorescences, *L. pusilla* (Figure 22 F) and *L. barkeriana*, and in *Polyxena* they were condensed into corymbose or subcorymbose inflorescences, i.e. the corymbose inflorescences of *P. ensifolia* (Figure 23 A), *P. maughanii* and *P. longituba*, and the subcorymbose inflorescences of *P. paucifolia* and most forms of *P. corymbosa* (Figure 23 B). *L. sargeantii* was the only species with a subcorymbose raceme borne on a long, aerial peduncle. In 32 (23%) *Lachenalia* taxa, the flowers were sessile, forming a spike (Figure 22A-C), and in five (4%) *Lachenalia* taxa (*L. capensis*, *L. karooica*, *L. longibracteata*, *L. marlothii* and *L. obscura*) the character was polymorphic within populations (Table 24). Inflorescence type was stable but in *L. trichophylla* it was stable only at subspecific level; thus the inflorescence of *L. trichophylla* subsp. *trichophylla* was a spike, whereas the subsp. *massonii* was a raceme. It was clear from the intraspecific variation within *L. trichophylla* that the genetic constraints on pedicel lengths were not particularly strong.



Figure 22. Variation in inflorescence type in *Lachenalia*. Spicate inflorescences of A, *L. framesii* (Duncan 99); B, *L. mutabilis* (Botha s.n.); C, *L. verticillata* (Müller-Doblies 88125). Racemose inflorescences of D, *L. contaminata* var. *exserta* (Malan 117); E, *L. variegata* (Duncan 392); subcapitate, racemose inflorescence of F, *L. pusilla* (Duncan 210); racemose inflorescences of G, *L. aloides* var. *aurea* (Duncan 363); H, *L. bolusii* (Duncan 256); I, *L. nardouwensis* (Duncan 198).

Scale bar = 20 mm.

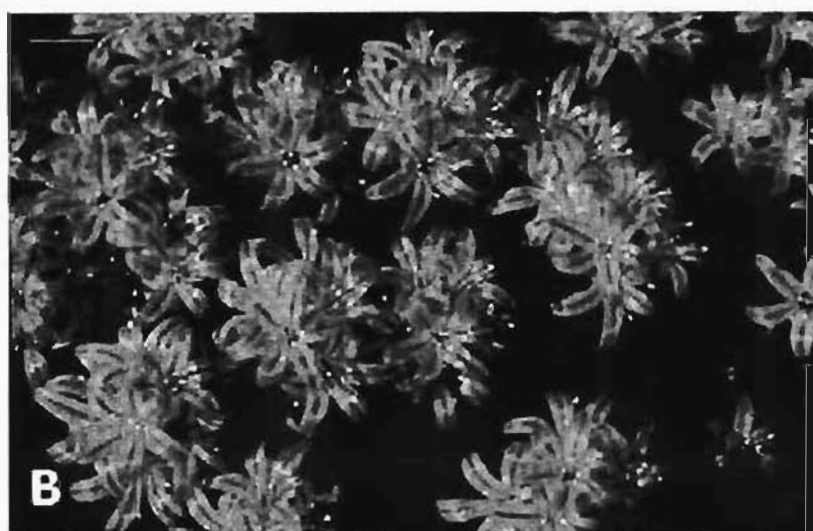


Figure 23. Variation in inflorescence type in *Polyxena*.

A, corymbose raceme of *P. ensifolia* (Duncan 427);

B, subcorymbose raceme of *P. corymbosa* (Simmons s.n.).

Scale bars: A = 16 mm, B = 9 mm.

Character State	Taxa
Racemose	<i>L. alba</i> , <i>L. algoensis</i> , <i>L. aloides</i> (all eight varieties), <i>L. angelica</i> , <i>L. anguinea</i> , <i>L. arida</i> , <i>L. attenuata</i> , <i>L. aurioliae</i> , <i>L. bachmannii</i> , <i>L. barkeriana</i> , <i>L. bolusii</i> , <i>L. bowkeri</i> , <i>L. buchubergensis</i> , <i>L. bulbifera</i> , <i>L. campanulata</i> , <i>L. cernua</i> , <i>L. comptonii</i> , <i>L. contaminata</i> (both varieties), <i>L. convallarioides</i> , <i>L. dasybotrya</i> , <i>L. dehoopensis</i> , <i>L. doleritica</i> , <i>L. duncanii</i> , <i>L. esterhuysenae</i> , <i>L. giessii</i> , <i>L. gillettii</i> , <i>L. glauca</i> , <i>L. glaucophylla</i> , <i>L. haarlemensis</i> , <i>L. hirta</i> (both varieties), <i>L. isopetala</i> , <i>L. juncifolia</i> (both varieties), <i>L. klinghardtiana</i> , <i>L. komsbergensis</i> , <i>L. lactosa</i> , <i>L. latimerae</i> , <i>L. leipoldtii</i> , <i>L. leomontana</i> , <i>L. liliiflora</i> , <i>L. macgregorium</i> , <i>L. margaretae</i> , <i>L. martinae</i> , <i>L. mathewsii</i> , <i>L. maximiliani</i> , <i>L. mediana</i> (both varieties), <i>L. moniliformis</i> , <i>L. montana</i> , <i>L. multifolia</i> , <i>L. namibiensis</i> , <i>L. nardouwensis</i> , <i>L. neilii</i> , <i>L. nervosa</i> , <i>L. nordenstamii</i> , <i>L. nutans</i> , <i>L. orthopetala</i> , <i>L. patula</i> , <i>L. pearsonii</i> , <i>L. peersii</i> , <i>L. perryae</i> , <i>L. physocaulos</i> , <i>L. polyphylla</i> , <i>L. polypodantha</i> , <i>L. purpureocaerulea</i> , <i>L. pusilla</i> , <i>L. pustulata</i> , <i>L. reflexa</i> , <i>L. rosea</i> , <i>L. rubida</i> , <i>L. salteri</i> , <i>L. sargeantii</i> , <i>L. schelpei</i> , <i>L. stayneri</i> , <i>L. thomasiae</i> , <i>L. trichophylla</i> subsp. <i>massonii</i> , <i>L. unicolor</i> , <i>L. unifolia</i> (both varieties), <i>L. variegata</i> , <i>L. violacea</i> , <i>L. viridiflora</i> , <i>L. whitehillensis</i> , <i>L. wiesei</i> , <i>L. xerophila</i> , <i>L. youngii</i> , <i>L. zebrina</i> , <i>L. zeyheri</i> <i>P. corymbosa</i> , <i>P. ensifolia</i> , <i>P. longituba</i> , <i>P. maughanii</i> , <i>L. paucifolia</i> <i>Massonia</i>
Spicate	<i>L. ameliae</i> , <i>L. arbutnotiae</i> , <i>canaliculata</i> , <i>L. carnosa</i> , <i>L. concordiana</i> , <i>L. congesta</i> , <i>L. elegans</i> (all four varieties), <i>L. fasciculata</i> , <i>L. fistulosa</i> , <i>L. framesii</i> , <i>L. inconspicua</i> , <i>L. kliprandensis</i> , <i>L. lutea</i> , <i>L. marginata</i> (both subspecies), <i>L. minima</i> , <i>L. muiirii</i> , <i>L. mutabilis</i> , <i>L. namaquensis</i> , <i>L. orchioides</i> (both varieties), <i>L. splendida</i> , <i>L. trichophylla</i> subsp. <i>trichophylla</i> , <i>L. undulata</i> (both subspecies), <i>L. urceolata</i> , <i>L. valeriae</i> , <i>L. ventricosa</i> , <i>L. verticillata</i>
Polymorphic	<i>L. capensis</i> , <i>L. karooica</i> , <i>L. longibracteata</i> , <i>L. marlothii</i> , <i>L. obscura</i>

2) **Pedicel orientation at anthesis.** Five states occurred: pedicels erect (=0); pedicels suberect (=1); pedicels patent (=2); pedicels curved downwards (=3); and pedicels absent (=4). Quantitative character, scored as character 37 (Appendix 1).

Erect pedicels occurred in *Massonia* and eight (6%) ingroup taxa (three *Lachenalia*, all five *Polyxena*) in which pedicels diverged from the rachis between five and 15 degrees. In 82 (59%) *Lachenalia* taxa the pedicels were suberect and diverged between 30 and 70 degrees from the rachis, in ten (7%) *Lachenalia* taxa pedicels were patent and diverged from the rachis between 80 and 90 degrees, and in three (2%) *Lachenalia* taxa pedicels were curved downwards, diverging from the rachis between 110 and 130 degrees (Figure 24, Table 25).

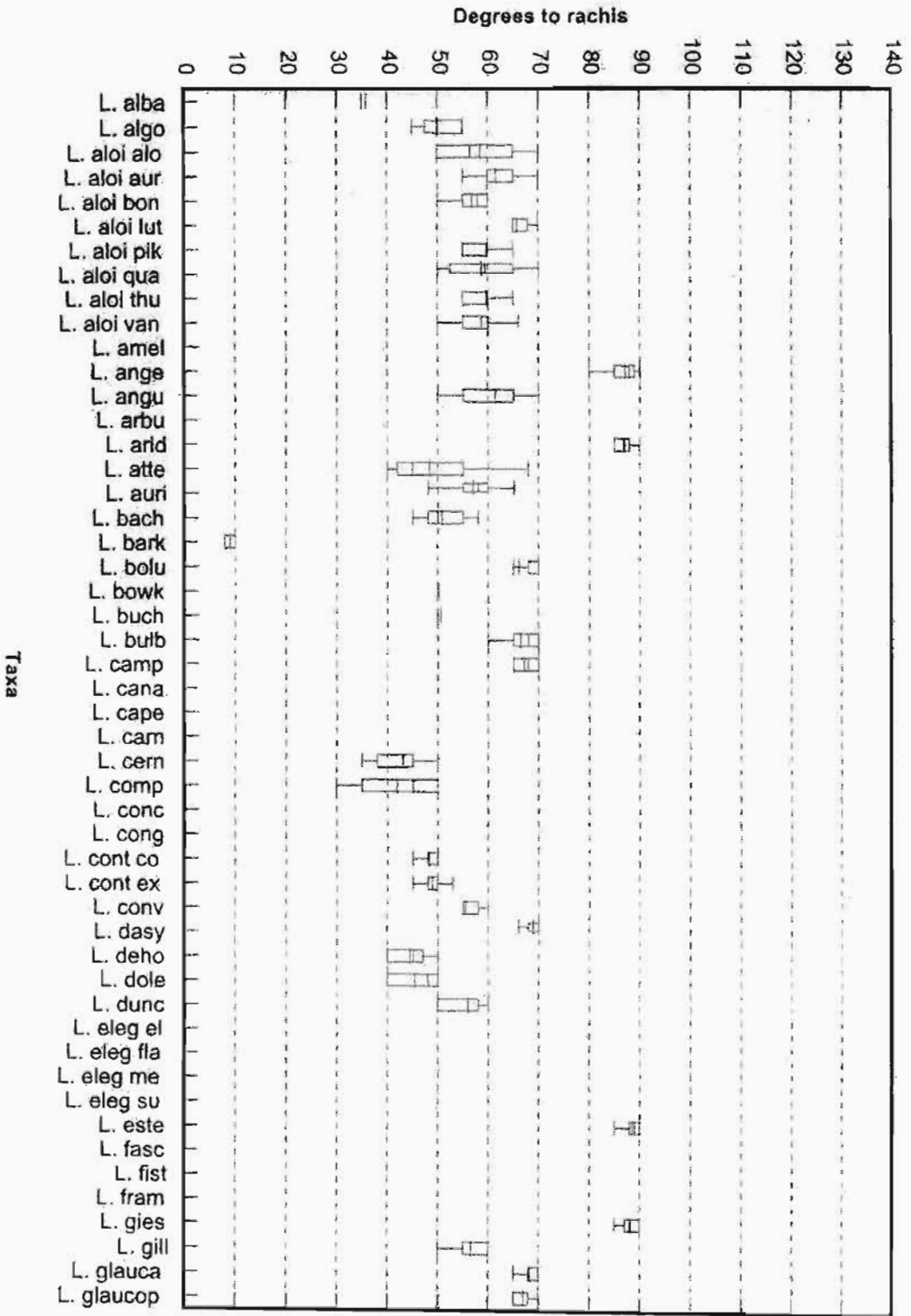


Figure 24. Pedicel orientation in *Lachenalia* and *Polyxena*

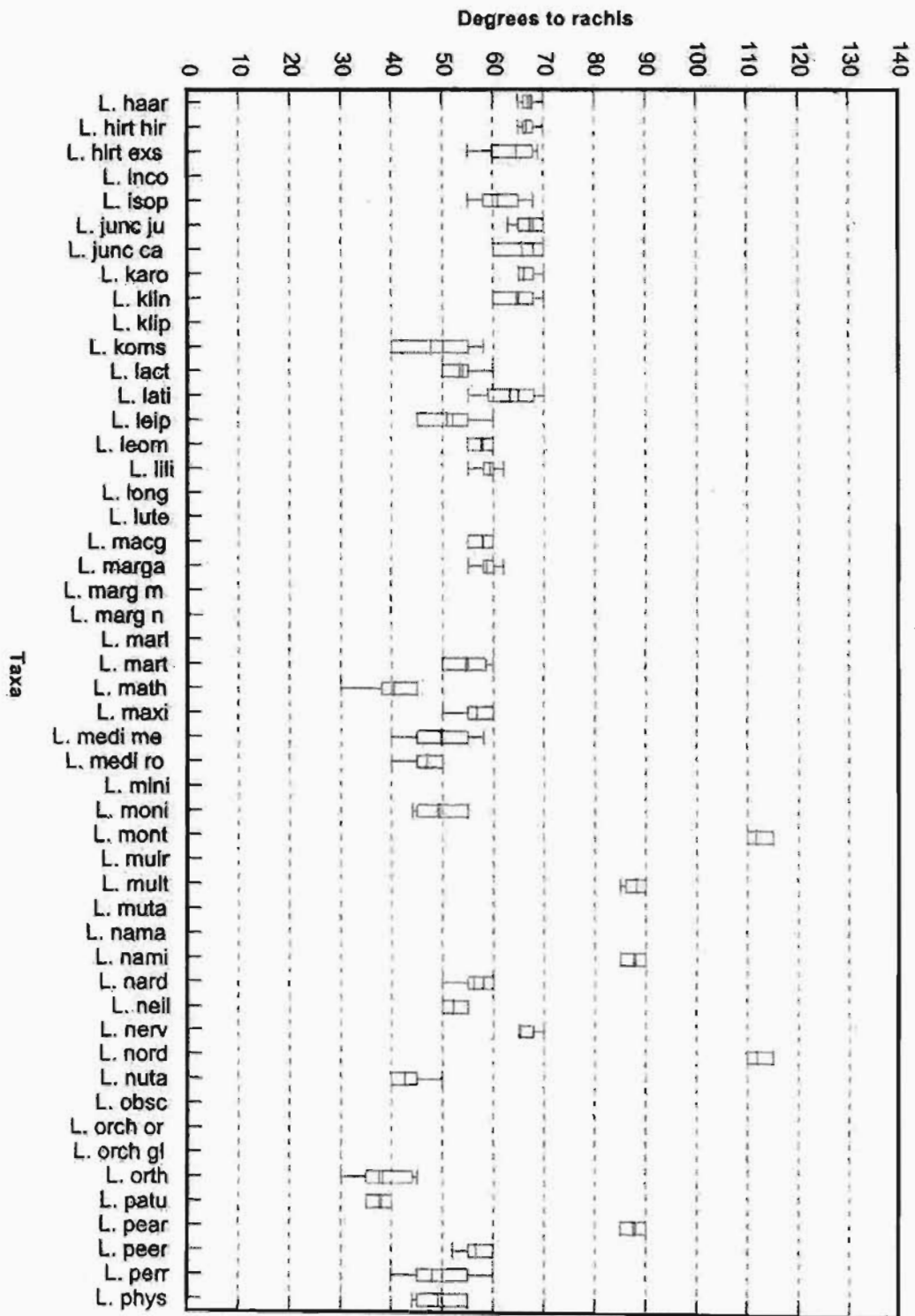


Figure 24. Pedicel orientation in Lachenalia and Polyxena

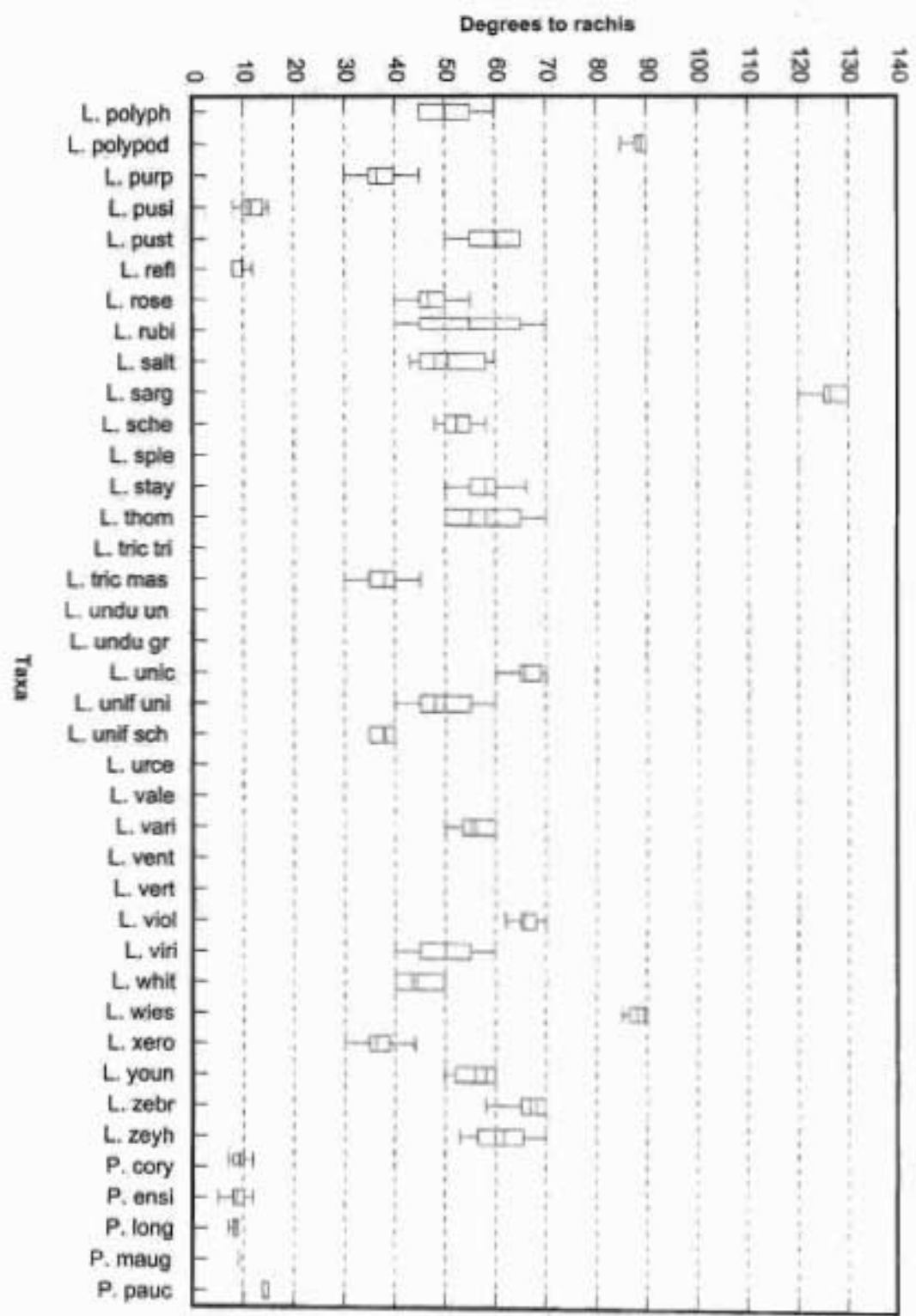


Figure 24. Pedicel orientation in Lichenalia and Polyxena

Character State	Taxa
Erect	<i>L. barkeriana</i> , <i>L. pusilla</i> , <i>L. reflexa</i> <i>P. corymbosa</i> , <i>P. ensifolia</i> , <i>P. longituba</i> , <i>P. maughanii</i> , <i>P. paucifolia</i> <i>Massonia</i>
Suberect	<i>L. alba</i> , <i>L. algoensis</i> , <i>L. aloides</i> (all eight varieties), <i>L. anguinea</i> , <i>L. attenuata</i> , <i>L. aurioliae</i> , <i>L. bachmannii</i> , <i>L. bolusii</i> , <i>L. bowkeri</i> , <i>L. buchbergensis</i> , <i>L. bulbifera</i> , <i>L. campanulata</i> , <i>L. cernua</i> , <i>L. comptonii</i> , <i>L. contaminata</i> (both varieties), <i>L. convallarioides</i> , <i>L. dasybotrya</i> , <i>L. dehoopensis</i> , <i>L. doleritica</i> , <i>L. duncanii</i> , <i>L. gillettii</i> , <i>L. glauca</i> , <i>L. glaucophylla</i> , <i>L. haarlemensis</i> , <i>L. hirta</i> (both varieties), <i>L. isopetala</i> , <i>L. juncifolia</i> var. <i>juncifolia</i> , <i>L. karooica</i> , <i>L. klinghardtiana</i> , <i>L. komsbergensis</i> , <i>L. lactosa</i> , <i>L. latimerae</i> , <i>L. leipoldtii</i> , <i>L. leomontana</i> , <i>L. liliiflora</i> , <i>L. macgregoriorum</i> , <i>L. margaretae</i> , <i>L. martiniae</i> , <i>L. mathewsii</i> , <i>L. maximiliani</i> , <i>L. mediana</i> (both varieties), <i>L. moniliformis</i> , <i>L. nardouwensis</i> , <i>L. neilii</i> , <i>L. nervosa</i> , <i>L. nutans</i> , <i>L. orthopetala</i> , <i>L. patula</i> , <i>L. peersii</i> , <i>L. perryae</i> , <i>L. physocaulos</i> , <i>L. polyphylla</i> , <i>L. purpureocaerulea</i> , <i>L. pustulata</i> , <i>L. rosea</i> , <i>L. rubida</i> , <i>L. salteri</i> , <i>L. schelpei</i> , <i>L. stayneri</i> , <i>L. thomasiae</i> , <i>L. trichophylla</i> subsp. <i>massonii</i> , <i>L. unicolor</i> , <i>L. unifolia</i> (both varieties), <i>L. variegata</i> , <i>L. violacea</i> , <i>L. viridiflora</i> , <i>L. whitehillensis</i> , <i>L. xerophila</i> , <i>L. youngii</i> , <i>L. zebrina</i> , <i>L. zeyheri</i>
Patent	<i>L. angelica</i> , <i>L. arida</i> , <i>L. estehuyensae</i> , <i>L. giessii</i> , <i>L. juncifolia</i> var. <i>campanulata</i> , <i>L. multifolia</i> , <i>L. namibiensis</i> , <i>L. pearsonii</i> , <i>L. polypodantha</i> , <i>L. wiesei</i>
Curved downwards	<i>L. montana</i> , <i>L. nordenstamii</i> , <i>L. sargeantii</i>
Pedicels absent	<i>L. ameliae</i> , <i>L. arbutnotiae</i> , <i>L. canaliculata</i> , <i>L. capensis</i> , <i>L. carnosa</i> , <i>L. concordiana</i> , <i>L. congesta</i> , <i>L. elegans</i> (all four varieties), <i>L. fasciculata</i> , <i>L. fistulosa</i> , <i>L. framesii</i> , <i>L. inconspicua</i> , <i>L. kliprandensis</i> , <i>L. longibracteata</i> , <i>L. lutea</i> , <i>L. marginata</i> (both subspecies), <i>L. marlothii</i> , <i>L. minima</i> , <i>L. muirii</i> , <i>L. mutabilis</i> , <i>L. namaquensis</i> , <i>L. obscura</i> , <i>L. orchioides</i> (both varieties), <i>L. splendida</i> , <i>L. trichophylla</i> subsp. <i>trichophylla</i> , <i>L. undulata</i> (both subspecies), <i>L. urceolata</i> , <i>L. valeriae</i> , <i>L. ventricosa</i> , <i>L. verticillata</i>

Pedicels were absent from 36 (26%) *Lachenalia* taxa. Pedicel length varied from 1 mm up to 20 mm. Pedicel colour was uniformly white in *Polyxena* and most *Lachenalia* species, but in some it was pale to dark green, yellow, mauve or magenta (*L. haarlemensis*, *L. mathewsii*, *L. pustulata*, *L. unicolor*, respectively).

5.10 PEDUNCLE

5.10.1 Results

The peduncles of all species of *Lachenalia* and *Polyxena* were smooth, and varied in length from 5 mm as in *L. barkeriana* and *P. maughanii*, up to 250 mm as in *L. anguinea* and *L. bulbifera*. Most species had peduncles between 10 and 20 mm. Peduncles were terete in all species but diameters and colours were highly variable. Peduncle diameter was usually constant for its entire length or increased slightly towards the apex. Peduncle diameter varied from 2 mm (*L. polyphylla*) up to 15 mm (*L. anguinea*) but in most species it varied between 3 and 5 mm. Peduncle colour ranged from pale to dark green in most species, and white in species with subterranean peduncles. Several species had uniformly deep brownish-magenta (*L. angelica*, *L. orthopetala*) or bright magenta (*L. patula*) peduncles. Phenotypic variation in peduncle colouration was marked, for example those of *L. montana* were uniformly green or brownish-purple within the same population. The peduncles of many species were variously blotched or spotted for their entire length. Blotch and spot size and colouring was highly variable, ranging from minute and dull magenta (up to 0.5 mm diameter, as in *L. polyphylla*) to medium-sized and bright magenta, dark brown or grey (up to 2 mm in diameter, as in *L. whitehillensis*, *L. lactosa*, *L. haarlemensis*, respectively), to very large and brown to deep purple (up to 4 mm in diameter, as in *L. zebrina*, certain forms of *L. violacea*). However, blotch and spot size did not form clearly discontinuous units as exceptions occurred within all the size ranges and so the character was excluded from the cladistic analyses. The peduncles of all species were covered with a delicate, powder-like bloom.

Two peduncle characters were defined for the cladistic analyses:

1) **Peduncle elevation at anthesis.** Two states occurred: subterranean peduncles (=0); and aerial peduncles (=1). Qualitative character, scored as character 28 (Appendix 1).

Subterranean peduncles occurred in *Massonia* and in seven (6%) *Lachenalia* and *Polyxena*

species (*L. barkeriana*, *L. congesta*, *L. kliprandensis*, *L. pusilla*, *P. ensifolia*, *P. longituba* and *P. maughanii*). Aerial peduncles occurred in 113 (94%) *Lachenalia* and *Polyxena* species (111 *Lachenalia*, *P. corymbosa*, *P. paucifolia*). Peduncle elevation was phenotypically plastic in *L. congesta* and *L. kliprandensis* as the subterranean state was occasionally lost under cultivation.

2) **Peduncle inflation.** Three states occurred: non-inflated peduncles (=0); inflated peduncles (=1); and polymorphic peduncles (=2). Qualitative character, scored as character 29 (Appendix 1).

In *Massonia* peduncles were not inflated, in which the diameter of the uppermost portion was the same as, or up to 2 mm broader than the lower portion, and this condition also occurred in 110 (92%) ingroup species (105 *Lachenalia*, all five *Polyxena*). In *Lachenalia* nine (7.5%) species had peduncles in which the uppermost portion was distinctly inflated and more than twice the diameter of the lower portion, *L. anguinea*, *L. barkeriana*, *L. glauca*, *L. klinghardtiana*, *L. mutans*, *L. physocaulos*, *L. ventricosa*, *L. violacea* and *L. xerophila*. In *L. mutabilis* the state was polymorphic, in which both non-inflated and inflated peduncles occurred within populations. Peduncle inflation was phenotypically plastic in *L. anguinea*, *L. klinghardtiana* and *L. violacea* as the inflated state was often reduced or lost in cultivated specimens.

5.11 RACHIS

5.11.1 Results

Rachis colour was similar to that of the peduncle in most *Lachenalia* and all *Polyxena* species, but in some it became paler towards the apex while in others it became much more intensely coloured towards the apex (e.g. *L. mutabilis* became pale blue or bright electric blue) (Figure 22B). In a number of species colour changes were abrupt, probably due to being governed by different genes (Vogelpoel 1986), (e.g. *L. aloides* var. *aurea* changed from deep brownish-purple to bright orange).

Rachis shape varied from slightly to distinctly angular but did not form clearly discontinuous classes and was not used in the cladistic analyses.

Four rachis characters were defined for the cladistic analyses:

1) **Rachis apical anthocyanins.** Two states occurred: anthocyanins absent (=0); and anthocyanins present (=1). Qualitative character, scored as character 30 (Appendix 1).

Anthocyanins were absent from the rachis apex of *Massonia*. Apical anthocyanin expression in the rachis was the most common condition in *Lachenalia* and *Polyxena*, and occurred in 123 (90%) taxa (121 *Lachenalia*, two *Polyxena*) of the 136 taxa investigated. Anthocyanins were absent in the inner and outer mesophyll of the rachis apex in 13 (10%) *Lachenalia* and *Polyxena* taxa (ten *Lachenalia*, three *Polyxena*), (*L. aloides* var. *aurea*, *L. aloides* var. *piketbergensis*, *L. angelica*, *L. arbuthnotiae*, *L. barkeriana*, *L. bowkeri*, *L. patula*, *L. pusilla*, *L. undulata* subsp. *undulata*, *L. undulata* subsp. *grandifolia*, *P. ensifolia*, *P. longituba* and *P. maughanii*).

2) **Rachis apical carotenoids.** Two states occurred: carotenoids absent (=0); and carotenoids present (=1). Qualitative character, scored as character 31 (Appendix 1).

The rachis apex of *Massonia* and 127 (93%) *Lachenalia* and *Polyxena* taxa of the 136 taxa investigated was devoid of attractive carotenoids. In nine (7%) *Lachenalia* taxa, apical carotenoids were present in both the inner and outer mesophyll (*L. aloides* var. *aurea*, *L. aloides* var. *piketbergensis* and *L. arbuthnotiae*), or only in the inner mesophyll (*L. aloides* var. *aloides*, *L. aloides* var. *bonaspei*, *L. aloides* var. *luteola*, *L. aloides* var. *quadricolor*, *L. aloides* var. *thunbergii* and *L. bulbifera*).

3) **Rachis apical chlorophylls.** Two states occurred: chlorophylls absent (=0), and chlorophylls present (=1). Qualitative character, scored as character 32 (Appendix 1).

Rachis apical chlorophylls were absent from *Massonia*, and 133 (98%) of the 136 *Lachenalia* and *Polyxena* taxa investigated. In three (2%) *Lachenalia* taxa, the rachis was green due to chlorophylls in the inner and outer mesophyll, *L. bowkeri*, *L. undulata* subsp. *undulata* and *L. undulata* subsp. *grandifolia*.

4) **Rachis apex structural white.** Two states occurred: structural colour present (=0), and structural colour absent (=1). Qualitative character, scored as character 33 (Appendix 1).

Aerenchymatous structural white occurred in the inner and outer mesophyll of *Massonia*, and in seven (5%) *Lachenalia* and *Polyxena* taxa out of the 136 taxa investigated, *L. angelica*, *L. barkeriana*, *L. patula*, *L. pusilla*, *P. ensifolia*, *P. longituba* and *P. maughanii*. In 129 (95%) taxa (127 *Lachenalia*, two *Polyxena*), structural reflectance was absent.

5.12 BRACTS

5.12.1 Results

Floral bracts with basal cupules occurred in all species of *Lachenalia* and *Polyxena*. The function of bracts is probably protection of the inflorescence while it is being pushed through other tissues of the substrate. They may also assume secondary functions such as pollinator attraction. They were uniform in colour within species; in *Polyxena* they were translucent and in *Lachenalia* they varied from translucent to white, green, brown, red or purple. There were two main bract shapes, triangular and obtuse. Triangular bracts had fleshy bases, and translucent, membranous upper parts, whereas obtuse bracts were fleshy throughout. *L. isopetala* was the only species with papery bracts. Species had various bract arrangements, and within these there was a range of shapes; bract structure varied within inflorescences and was treated as a set of character states. Most species had triangular bracts, and within this group there were two subtypes. In the largest subtype the bracts in the lower portion of the inflorescence were ovate to broadly ovate, becoming progressively longer and narrower towards the middle and upper parts of the inflorescence, with narrowly lanceolate bracts at the apex. A small subtype had ovate bracts throughout the inflorescence, which became progressively smaller towards the apex. Obtuse, cup-shaped bracts were the second major type. These occurred throughout inflorescences but were relatively large at the base and became progressively smaller towards the top.

Bract size was highly variable in *Lachenalia*, ranging from minute, inconspicuous basal bracts 1 x 1 mm (*L. polypodantha*, *L. zebrina*) to relatively large basal bracts 6 x 4 mm (*L. bulbifera*). Uppermost bract length reached 16 mm long in some species, as in *L. longibracteata* and *L. undulata*. Bract size did not resolve into clearly discontinuous evolutionary classes and was thus not selected for use in the cladistic analyses.

Two bract characters were defined for the cladistic analyses:

1) **Lower bract shape.** Two states occurred: ovate (=0); and cup-shaped (=1). Qualitative character, scored as character 34 (Appendix 1).

Massonia shared ovate lower bracts with 101 (84%) ingroup species (96 *Lachenalia*, all five *Polyxena*). Cup-shaped lower bracts occurred in 19 (16%) *Lachenalia* species (Table 26).

2) **Upper bract shape.** Three states occurred: lanceolate (=0); ovate (=1); and cup-shaped (=2). Qualitative character, scored as character 35 (Appendix 1).

Lanceolate upper bracts occurred in *Massonia*, along with 71 (59%) ingroup species (66 *Lachenalia*, all five *Polyxena*). In 30 (25%) *Lachenalia* species the upper bracts were ovate, and in 19 (16%) species they were cup-shaped (Table 26).

Table 26. Variation in lower and upper bract shape in *Lachenalia*, *Polyxena* and the outgroup *Massonia*

Character state		Species
L O W E R B R A C T S	Ovate	<i>L. alba</i> , <i>L. algoensis</i> , <i>L. aloides</i> (all eight varieties), <i>L. ameliae</i> , <i>L. anguinea</i> , <i>L. arbutnotiae</i> , <i>L. attenuata</i> , <i>L. aurioliae</i> , <i>L. barkeriana</i> , <i>L. bolusii</i> , <i>L. bowkeri</i> , <i>L. buchbergensis</i> , <i>L. bulbifera</i> , <i>L. canaliculata</i> , <i>L. capensis</i> , <i>L. carnosa</i> , <i>L. cernua</i> , <i>L. concordiana</i> , <i>L. congesta</i> , <i>L. dasybotrya</i> , <i>L. dehoopensis</i> , <i>L. doleritica</i> , <i>L. duncanii</i> , <i>L. elegans</i> (all four varieties), <i>L. esterhuysenae</i> , <i>L. fasciculata</i> , <i>L. fistulosa</i> , <i>L. framesii</i> , <i>L. gillettii</i> , <i>L. glauca</i> , <i>L. haarlemensis</i> , <i>L. hirta</i> (both varieties), <i>L. inconspicua</i> , <i>L. isopetala</i> , <i>L. juncifolia</i> (both varieties), <i>L. karooica</i> , <i>L. klinghardtiana</i> , <i>L. kliprandensis</i> , <i>L. komsbergensis</i> , <i>L. lactosa</i> , <i>L. latimerae</i> , <i>L. leipoldtii</i> , <i>L. leomontana</i> , <i>L. longibracteata</i> , <i>L. lutea</i> , <i>L. margaretae</i> , <i>L. marginata</i> (both subspecies), <i>L. marlothii</i> , <i>L. martinae</i> , <i>L. mathewsii</i> , <i>L. maximiliani</i> , <i>L. mediana</i> (both varieties), <i>L. minima</i> , <i>L. moniliformis</i> , <i>L. montana</i> , <i>L. muirii</i> , <i>L. mutabilis</i> , <i>L. namaquensis</i> , <i>L. nardouwensis</i> , <i>L. neilii</i> , <i>L. nervosa</i> , <i>L. nordenstamii</i> , <i>L. nutans</i> , <i>L. obscura</i> , <i>L. orchioides</i> (both varieties), <i>L. peersii</i> , <i>L. perryae</i> , <i>L. physocaulos</i> , <i>L. purpureocaeerulea</i> , <i>L. pusilla</i> , <i>L. pustulata</i> , <i>L. reflexa</i> , <i>L. rosea</i> , <i>L. rubida</i> , <i>L. salteri</i> , <i>L. sargeantii</i> , <i>L. schelpei</i> , <i>L. splendida</i> , <i>L. stayneri</i> , <i>L. thomasiae</i> , <i>L. trichophylla</i> (both subspecies), <i>L. undulata</i> (both subspecies), <i>L. unicolor</i> , <i>L. unifolia</i> (both varieties), <i>L. urceolata</i> , <i>L. valeriae</i> , <i>L. variegata</i> , <i>L. ventricosa</i> , <i>L. verticillata</i> , <i>L. violacea</i> , <i>L. viridiflora</i> , <i>L. whitehillensis</i> , <i>L. wiesei</i> , <i>L. xerophila</i> , <i>L. youngii</i> , <i>L. zebrina</i> <i>P. corymbosa</i> , <i>P. ensifolia</i> , <i>P. longituba</i> , <i>P. maughanii</i> , <i>P. paucifolia</i> <i>Massonia</i>
	Cup-shaped	<i>L. angelica</i> , <i>L. arida</i> , <i>L. bachmannii</i> , <i>L. campanulata</i> , <i>L. comptonii</i> , <i>L. contaminata</i> (both varieties), <i>L. convallarioides</i> , <i>L. giessii</i> , <i>L. glaucophylla</i> , <i>L. liliiflora</i> , <i>L. macgregoriorum</i> , <i>L. multifolia</i> , <i>L. namibiensis</i> , <i>L. orthopetala</i> , <i>L. patula</i> , <i>L. pearsonii</i> , <i>L. polyphylla</i> , <i>L. polypodantha</i> , <i>L. zeyheri</i>
U P P E R B R A C T S	Lanceolate	<i>L. algoensis</i> , <i>L. aloides</i> (all eight varieties), <i>L. anguinea</i> , <i>L. arbutnotiae</i> , <i>L. bowkeri</i> , <i>L. buchbergensis</i> , <i>L. capensis</i> , <i>L. carnosa</i> , <i>L. cernua</i> , <i>L. concordiana</i> , <i>L. congesta</i> , <i>L. dasybotrya</i> , <i>L. dehoopensis</i> , <i>L. doleritica</i> , <i>L. duncanii</i> , <i>L. elegans</i> (all four varieties), <i>L. fistulosa</i> , <i>L. framesii</i> , <i>L. gillettii</i> , <i>L. hirta</i> (both varieties), <i>L. inconspicua</i> , <i>L. karooica</i> , <i>L. klinghardtiana</i> , <i>L. kliprandensis</i> , <i>L. komsbergensis</i> , <i>L. lactosa</i> , <i>L. leipoldtii</i> , <i>L. leomontana</i> , <i>L. longibracteata</i> , <i>L. lutea</i> , <i>L. margaretae</i> , <i>L. marginata</i> (both subspecies), <i>L. marlothii</i> , <i>L. martinae</i> , <i>L. maximiliani</i> , <i>L. mediana</i> (both varieties), <i>L. minima</i> , <i>L. montana</i> , <i>L. mutabilis</i> , <i>L. nardouwensis</i> , <i>L. nervosa</i> , <i>L. nordenstamii</i> , <i>L. nutans</i> , <i>L. orchioides</i> (both varieties), <i>L. peersii</i> , <i>L. physocaulos</i> , <i>L. pustulata</i> , <i>L. reflexa</i> , <i>L. rosea</i> , <i>L. salteri</i> , <i>L. sargeantii</i> , <i>L. schelpei</i> , <i>L. splendida</i> , <i>L. stayneri</i> , <i>L. thomasiae</i> , <i>L. undulata</i> (both subspecies), <i>L. unicolor</i> , <i>L. unifolia</i> (both varieties), <i>L. urceolata</i> , <i>L. valeriae</i> , <i>L. variegata</i> , <i>L. ventricosa</i> , <i>L. verticillata</i> , <i>L. viridiflora</i> , <i>L. xerophila</i> , <i>L. youngii</i> <i>P. corymbosa</i> , <i>P. ensifolia</i> , <i>P. longituba</i> , <i>P. maughanii</i> , <i>P. paucifolia</i> <i>Massonia</i>
	Ovate	<i>L. alba</i> , <i>L. ameliae</i> , <i>L. attenuata</i> , <i>L. aurioliae</i> , <i>L. barkeriana</i> , <i>L. bolusii</i> , <i>L. bulbifera</i> , <i>L. canaliculata</i> , <i>L. esterhuysenae</i> , <i>L. fasciculata</i> , <i>L. glauca</i> , <i>L. haarlemensis</i> , <i>L. isopetala</i> , <i>L. juncifolia</i> (both varieties), <i>L. latimerae</i> , <i>L. mathewsii</i> , <i>L. moniliformis</i> , <i>L. muirii</i> , <i>L. namaquensis</i> , <i>L. neilii</i> , <i>L. obscura</i> , <i>L. perryae</i> , <i>L. purpureocaeerulea</i> , <i>L. pusilla</i> , <i>L. rubida</i> , <i>L. trichophylla</i> (both subspecies), <i>L. violacea</i> , <i>L. whitehillensis</i> , <i>L. wiesei</i> , <i>L. zebrina</i>
	Cup-shaped	<i>L. angelica</i> , <i>L. arida</i> , <i>L. bachmannii</i> , <i>L. campanulata</i> , <i>L. comptonii</i> , <i>L. contaminata</i> (both varieties), <i>L. convallarioides</i> , <i>L. giessii</i> , <i>L. glaucophylla</i> , <i>L. liliiflora</i> , <i>L. macgregoriorum</i> , <i>L. multifolia</i> , <i>L. namibiensis</i> , <i>L. orthopetala</i> , <i>L. patula</i> , <i>L. pearsonii</i> , <i>L. polyphylla</i> , <i>L. polypodantha</i> , <i>L. zeyheri</i>

5.13 PERIANTH

5.13.1 Results

Perianth shape was the product of tepal posture, tepal shape and floral symmetry, and was extremely variable. The tepals of all *Lachenalia* and *Polyxena* species were biserate, arranged as inner and outer whorls of three. Divergence in perianth shape appeared to be driven by adaptation to a number of pollination vectors including sunbirds and bees.

Overall flower size varied from the minute, widely campanulate flowers of *L. glaucophylla* (5 x 6 mm), to the comparatively long, tubular flowers of *L. aloides* var. *piketbergensis* (30 x 10 mm). Perianth length varied considerably intraspecifically within variable species like *L. aloides* and *L. bulbifera*. Flower size did not form clearly discontinuous classes and was not used in the cladistic analyses.

The apical region of the outer tepals of most species had a single swelling known as a gibbosity. The size of this structure varied from small and inconspicuous (1 x 1 mm, *L. fistulosa*, *L. minima*) to relatively large and prominent (2-3 x 2-3 mm, *L. marginata*, *L. muirii*). Gibbosity colour varied from pale to dark green in most species through pale magenta to deep pink or maroon, and many shades of brown. The median keels of the inner tepals usually matched the gibbosity in colour. Gibbosity size was stable within species but gibbosity colouration was variable in many species. Discontinuous evolutionary states were not evident in gibbosity size and the character was thus not used in the cladistic analyses.

All *Lachenalia* and *Polyxena* species were gamotepalous, the tepals were fused at their bases to form a cup or flat disc, or a short to long tube. The base of the perianth tube arose obliquely from the peduncle or pedicel in most *Lachenalia* species. In actinomorphic flowers (all *Polyxena* species and *L. pearsonii*) the perianth tube arose radially.

The open flowers of most species were borne in a suberect, patent or cernuous position, as in *L. framesii* (Figure 22A), *L. ventricosa* and *L. nutans*, respectively, with smaller groups bearing erect flowers e.g. *L. barkeriana*, *L. reflexa*, *P. ensifolia* (Figure 23A), and pendulous flowers e.g. *L. aloides* (Figure 22G), *L. sargeantii*. Flower posture did not form clearly discontinuous classes and was not used in the cladistic analyses. Buds of all *Lachenalia* and *Polyxena* species were borne in an erect or suberect position. The terminal flowers of all *Lachenalia* and *Polyxena* species were much smaller than those below, and were sterile. They were frequently of more intense colouration than those on the rest of the inflorescence, as in *L. mutabilis* and *L. aloides* var. *aurea* (Figure 22 B,G), and probably assist in pollinator attraction. In certain species which had sessile flowers such as *L. mutabilis*, the terminal, sterile flowers often became distinctly pedicellate (Figure 22 B). The flowers of all *Lachenalia* and *Polyxena* species were acropetalous.

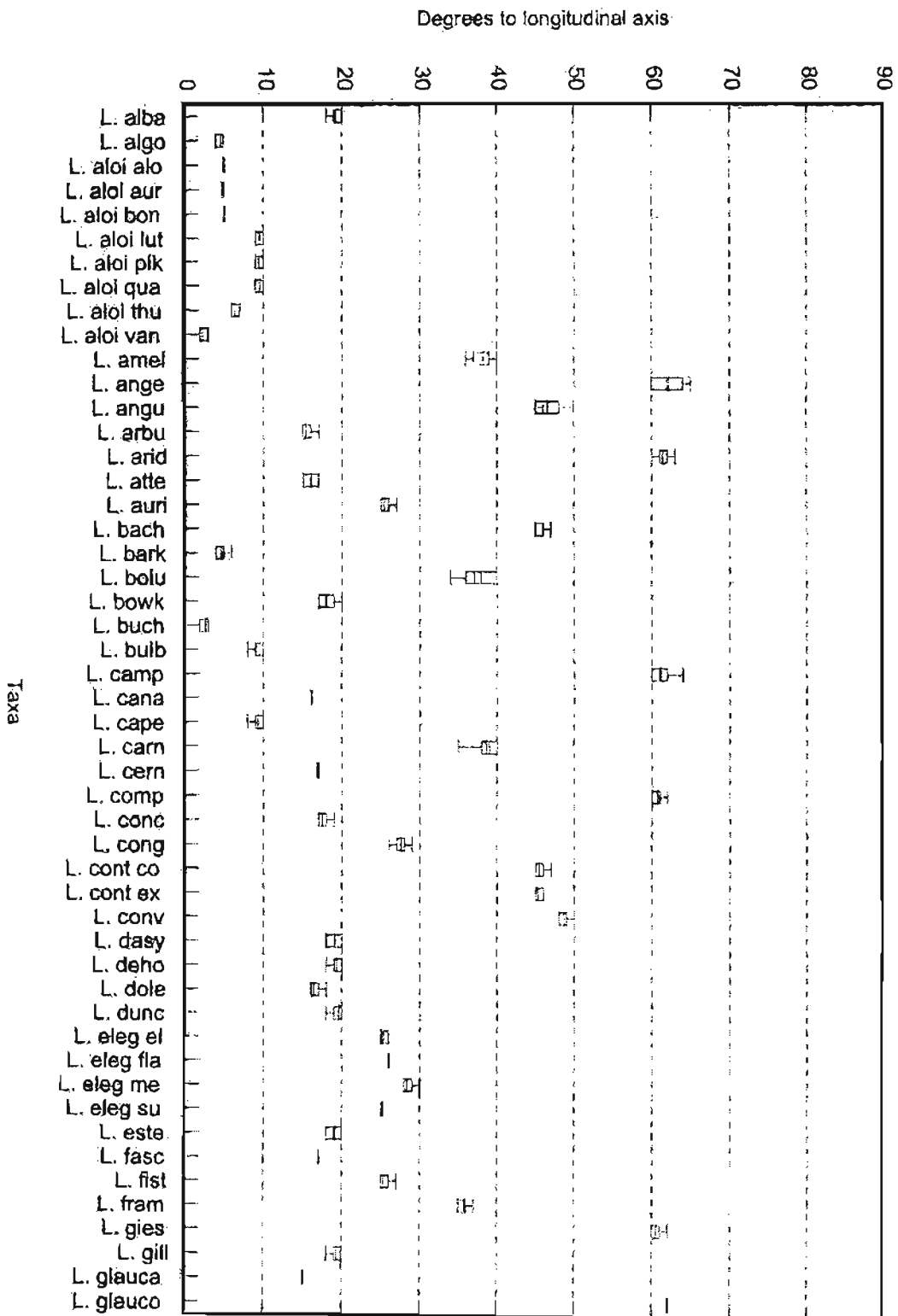
Many *Lachenalia* species had dull-coloured flowers in shades of green and brown which is a defensive mechanism to minimise the attention of predators. Widespread species varied considerably with respect to perianth length, flower colour and flowering period. The perianth length in forms of *L. bulbifera* in the southern and eastern parts of its distribution range was considerably shorter than those occurring in the western parts of its range. Similarly, flowering period varied markedly between the southern and eastern (early-flowering) parts, and the western (mid-season to late-flowering) parts of its range. Where possible such variation has been accommodated within the matrix.

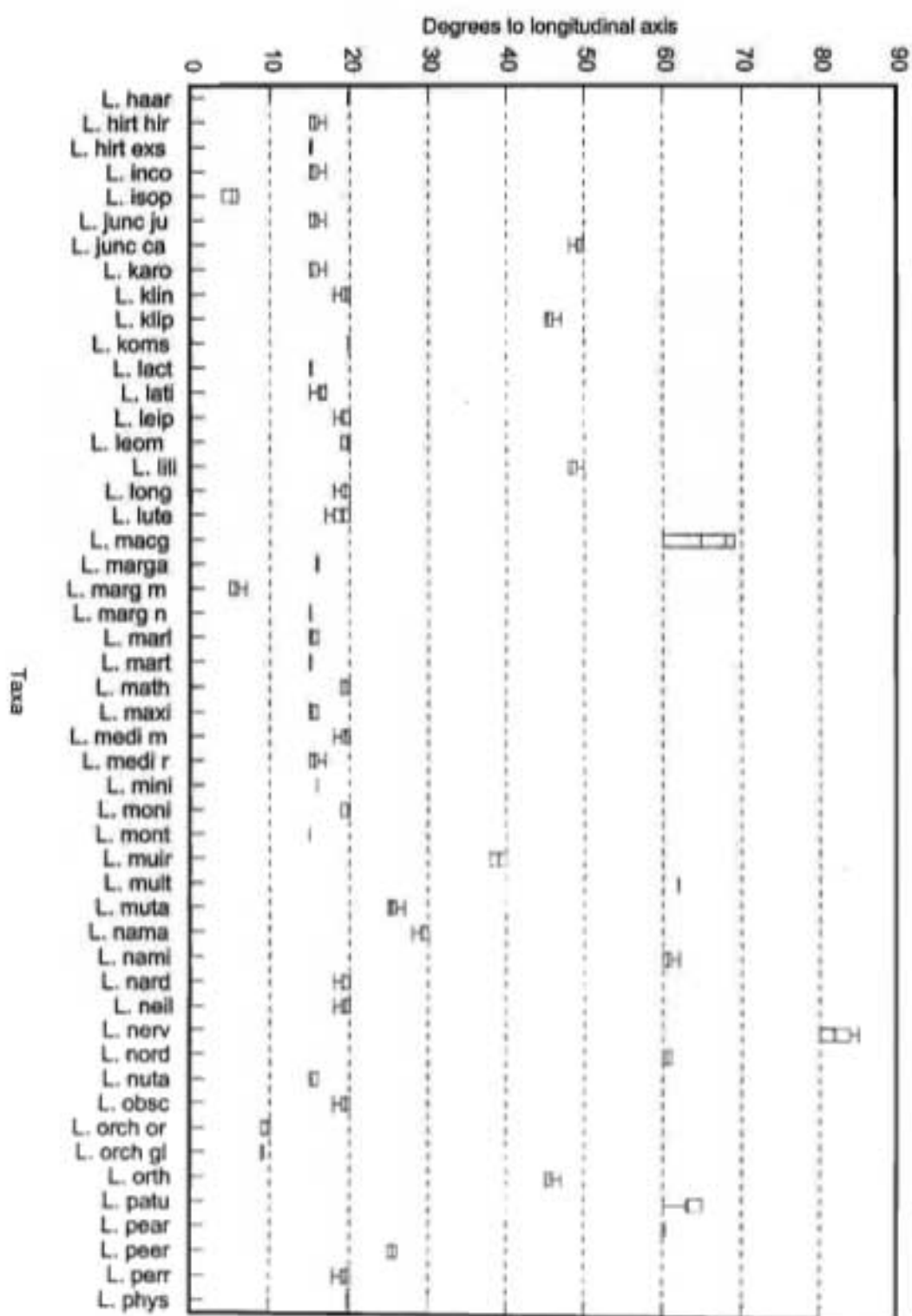
Twelve floral characters were defined for the cladistic analyses:

1) **Perianth shape (tepal orientation)**. Five states occurred: tubular (=0); oblong-campanulate (=1); narrowly campanulate (=2); widely campanulate (=3); and urceolate (=4). Quantitative character, scored as character 38 (Appendix 1).

Tubular perianths occurred in *Massonia*. Thirty-one (22%) ingroup taxa (26 *Lachenalia*, all five *Polyxena*) had tubular perianths (Figure 25A); in the 26 *Lachenalia* taxa the inner and outer tepals radiated up to 10 degrees from the longitudinal axis, or converged (*L. reflexa*, *L. schelpei*), but perianth shape in all five *Polyxena* taxa was anomalous in that although tepal orientation conformed to the widely campanulate character state, perianth shape was nevertheless scored as tubular by virtue of the tubular overall shape of their perianths (Figure 23A, B). In 66 (47%) *Lachenalia* taxa the perianth was oblong-campanulate (Figure 25B), with the outer tepals straight or weakly convex, and the inner tepals radiated at an angle of 15-20 degrees from the longitudinal axis. In 10 (7%) *Lachenalia* taxa the perianth was narrowly campanulate, and the inner and outer tepals radiated at an angle of 45-50 degrees from the longitudinal axis (Figure 25C). The perianth was widely campanulate in 14 (10%) *Lachenalia* taxa, and the inner and outer tepals radiated at an angle of 60-85 degrees from the longitudinal axis (Figure 25D). In 18 (13%) *Lachenalia* taxa the perianth was urceolate, and the outer and inner tepals converged. Here the inner tepals were contracted at the mouth and then radiated at an angle of 25-40 degrees from the longitudinal axis, with the inner tepals distinctly recurved (Figures 25E, 26, Table 27).



Figure 26. Perianth shape (tepal orientation) in *Lachenalia* and *Polyxena*

Figure 26. Perianth shape (tepal orientation) in *Lachenalia* and *Polyxena*

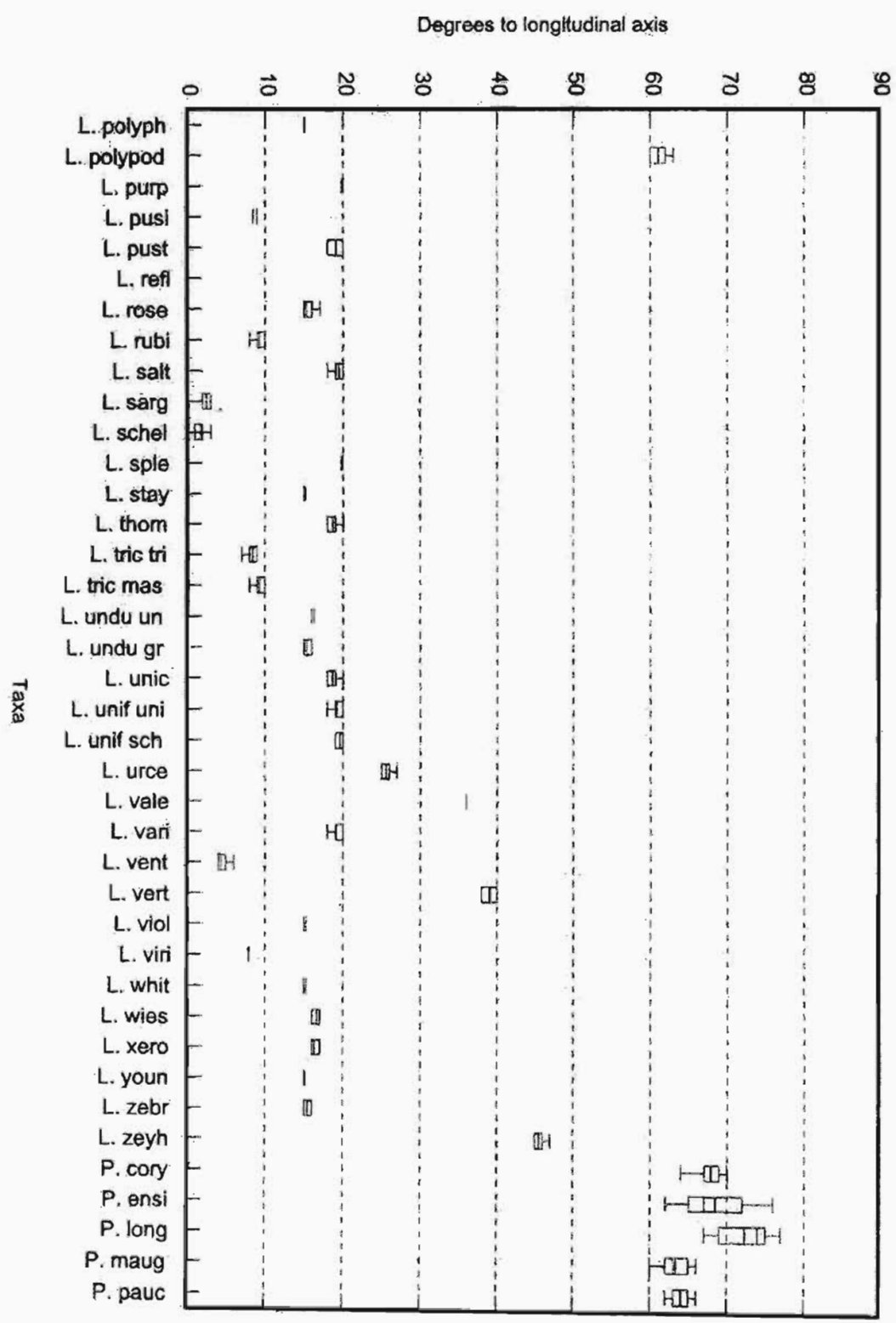


Figure 26. Perianth shape (tepal orientation) in *Lachenalia* and *Polyxena*

Character State	Taxa
Tubular	<i>L. algoensis</i> , <i>L. aloides</i> (all eight varieties), <i>L. barkeriana</i> , <i>L. buchbergensis</i> , <i>L. bulbifera</i> , <i>L. capensis</i> , <i>L. isopetala</i> , <i>L. marginata</i> subsp. <i>marginata</i> , <i>L. orchioides</i> (both varieties), <i>L. pusilla</i> , <i>L. reflexa</i> , <i>L. rubida</i> , <i>L. sargeantii</i> , <i>L. schelpei</i> , <i>L. trichophylla</i> (both subspecies), <i>L. ventricosa</i> , <i>L. viridiflora</i> <i>P. corymbosa</i> , <i>P. ensifolia</i> , <i>P. longituba</i> , <i>P. maughanii</i> , <i>P. paucifolia</i> <i>Massonia</i>
Oblong-campanulate	<i>L. alba</i> , <i>L. arbutnotiae</i> , <i>L. attenuata</i> , <i>L. bowkeri</i> , <i>L. canaliculata</i> , <i>L. cernua</i> , <i>L. concordiana</i> , <i>L. dasybotrya</i> , <i>L. dehoopensis</i> , <i>L. doleritica</i> , <i>L. duncanii</i> , <i>L. esterhuysenae</i> , <i>L. fasciculata</i> , <i>L. gillettii</i> , <i>L. glauca</i> , <i>L. haarlemensis</i> , <i>L. hirta</i> (both varieties), <i>L. inconspicua</i> , <i>L. juncifolia</i> var. <i>juncifolia</i> , <i>L. karooica</i> , <i>L. klinghardtiana</i> , <i>L. komsbergensis</i> , <i>L. lactosa</i> , <i>L. latimerae</i> , <i>L. leipoldtii</i> , <i>L. leomontana</i> , <i>L. longibracteata</i> , <i>L. lutea</i> , <i>L. margaretae</i> , <i>L. marginata</i> subsp. <i>neglecta</i> , <i>L. marlothii</i> , <i>L. martiniae</i> , <i>L. mathewsii</i> , <i>L. maximiliani</i> , <i>L. mediana</i> (both varieties), <i>L. minima</i> , <i>L. moniliformis</i> , <i>L. montana</i> , <i>L. nardouwensis</i> , <i>L. neilii</i> , <i>L. nutans</i> , <i>L. obscura</i> , <i>L. perryae</i> , <i>L. physocaulos</i> , <i>L. polyphylla</i> , <i>L. purpureocaerulea</i> , <i>L. pustulata</i> , <i>L. rosea</i> , <i>L. salteri</i> , <i>L. splendida</i> , <i>L. stayneri</i> , <i>L. thomasiae</i> , <i>L. undulata</i> (both subspecies), <i>L. unicolor</i> , <i>L. unifolia</i> (both varieties), <i>L. variegata</i> , <i>L. violacea</i> , <i>L. whitehillensis</i> , <i>L. wiesei</i> , <i>L. xerophila</i> , <i>L. youngii</i> , <i>L. zebrina</i>
Narrowly campanulate	<i>L. anguinea</i> , <i>L. bachmannii</i> , <i>L. contaminata</i> (both varieties), <i>L. convallarioides</i> , <i>L. juncifolia</i> var. <i>campanulata</i> , <i>L. kliprandensis</i> , <i>L. liliiflora</i> , <i>L. orthopetala</i> , <i>L. zeyheri</i>
Widely campanulate	<i>L. angelica</i> , <i>L. arida</i> , <i>L. campanulata</i> , <i>L. comptonii</i> , <i>L. giessii</i> , <i>L. glaucophylla</i> , <i>L. macgregoriorum</i> , <i>L. multifolia</i> , <i>L. namibiensis</i> , <i>L. nervosa</i> , <i>L. nordenstamii</i> , <i>L. patula</i> , <i>L. pearsonii</i> , <i>L. polypodantha</i>
Urceolate	<i>L. ameliae</i> , <i>L. aurioliae</i> , <i>L. bolusii</i> , <i>L. carnosa</i> , <i>L. congesta</i> , <i>L. elegans</i> (all four varieties), <i>L. fistulosa</i> , <i>L. framesii</i> , <i>L. muirii</i> , <i>L. mutabilis</i> , <i>L. namaquensis</i> , <i>L. peersii</i> , <i>L. urceolata</i> , <i>L. valeriae</i> , <i>L. verticillata</i>

2) **Perianth tube length.** Two discontinuous groups were recognised: long tubes (=0); and short tubes (=1). Quantitative character, scored as character 39 (Appendix 1).

Massonia and 23 (17%) ingroup taxa (18 *Lachenalia*, all five *Polyxena*) had long perianth tubes 6-25 mm long (Figures 23A, 25A). One hundred and sixteen (83%) *Lachenalia* taxa had short perianth tubes up to 3 mm long (Figures 25B-E, 27, Table 28).

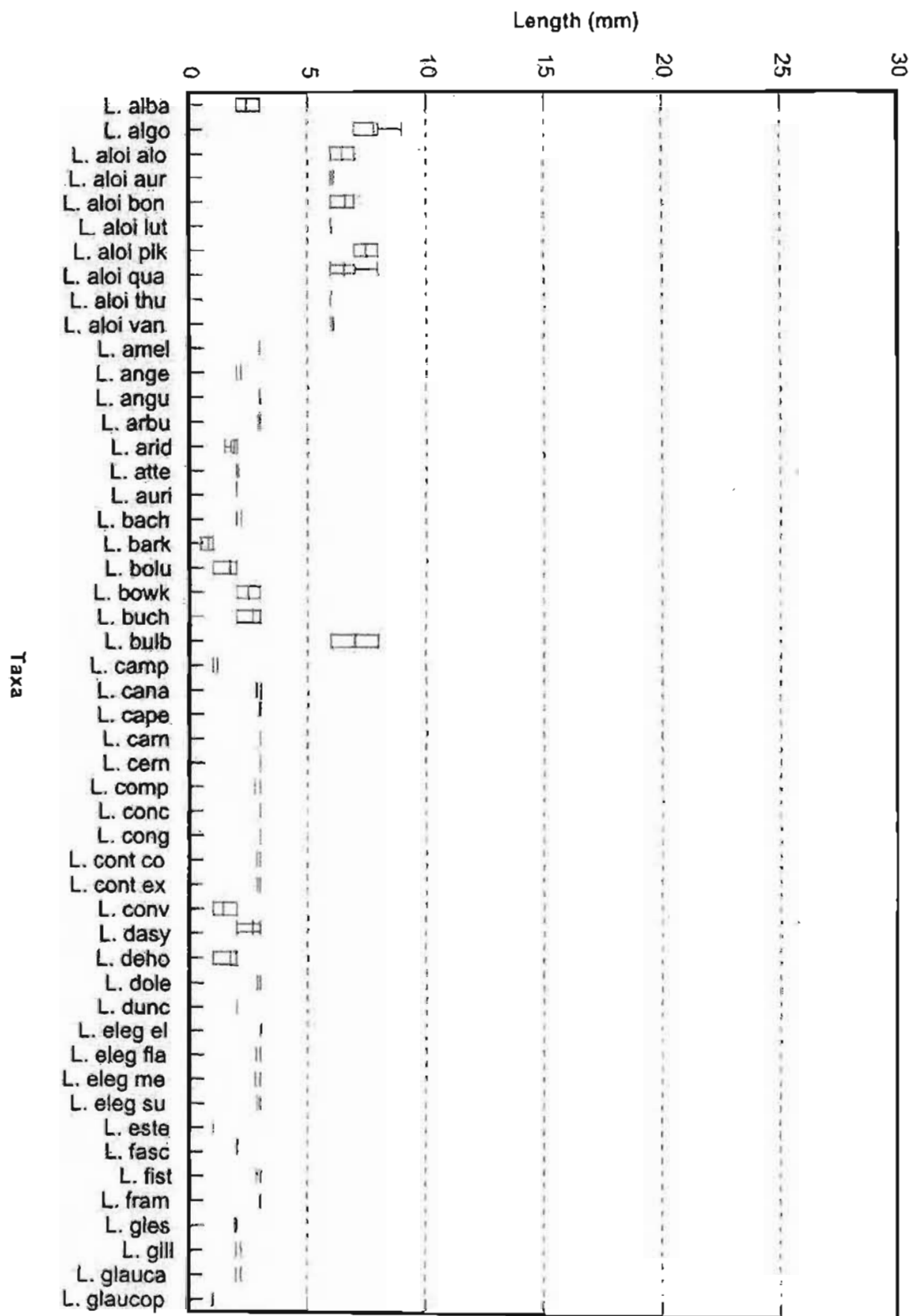


Figure 27. Perianth tube length in Lachenalia and Polyxena

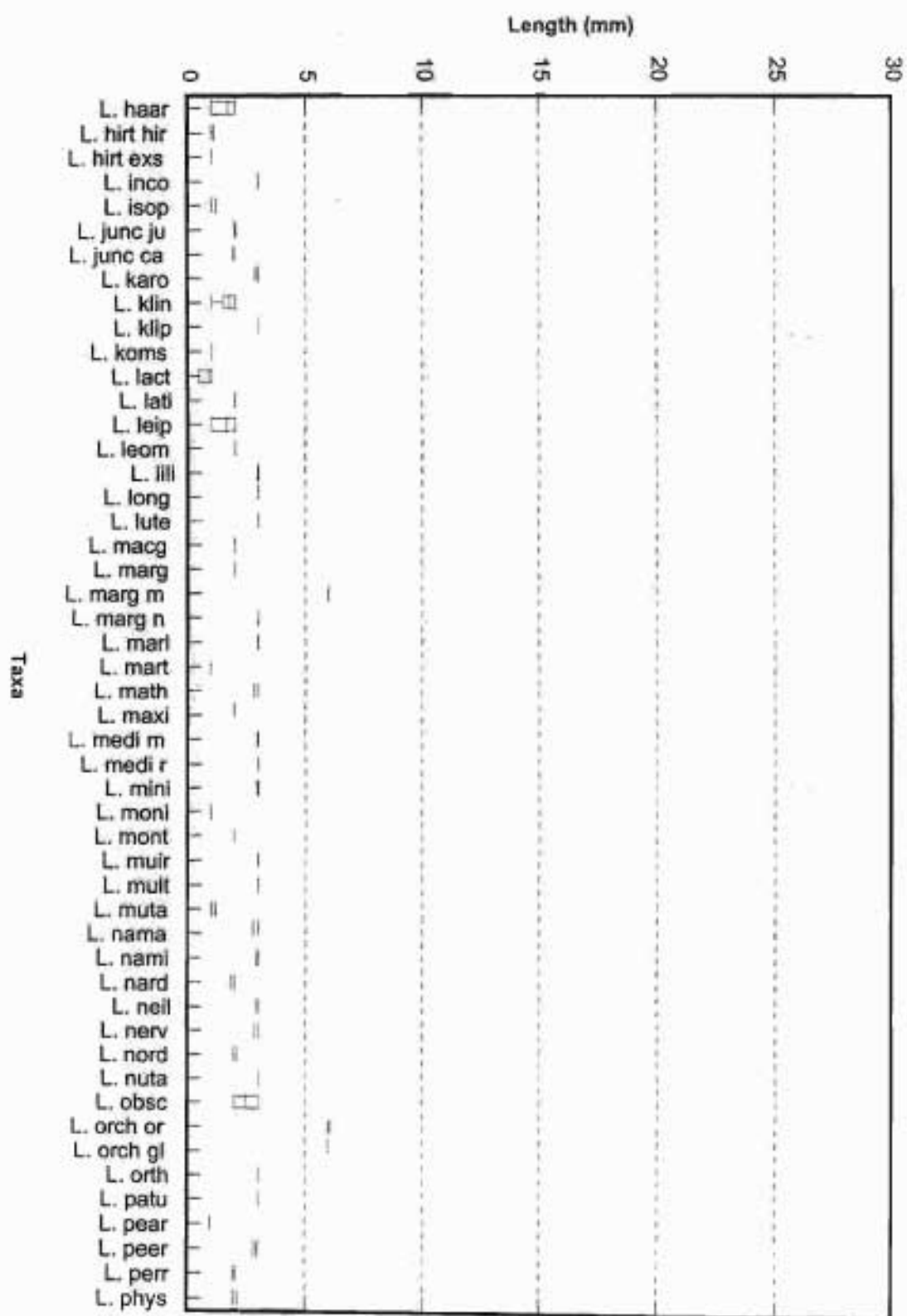


Figure 27. Perianth tube length in *Lachenalia* and *Polyxena*

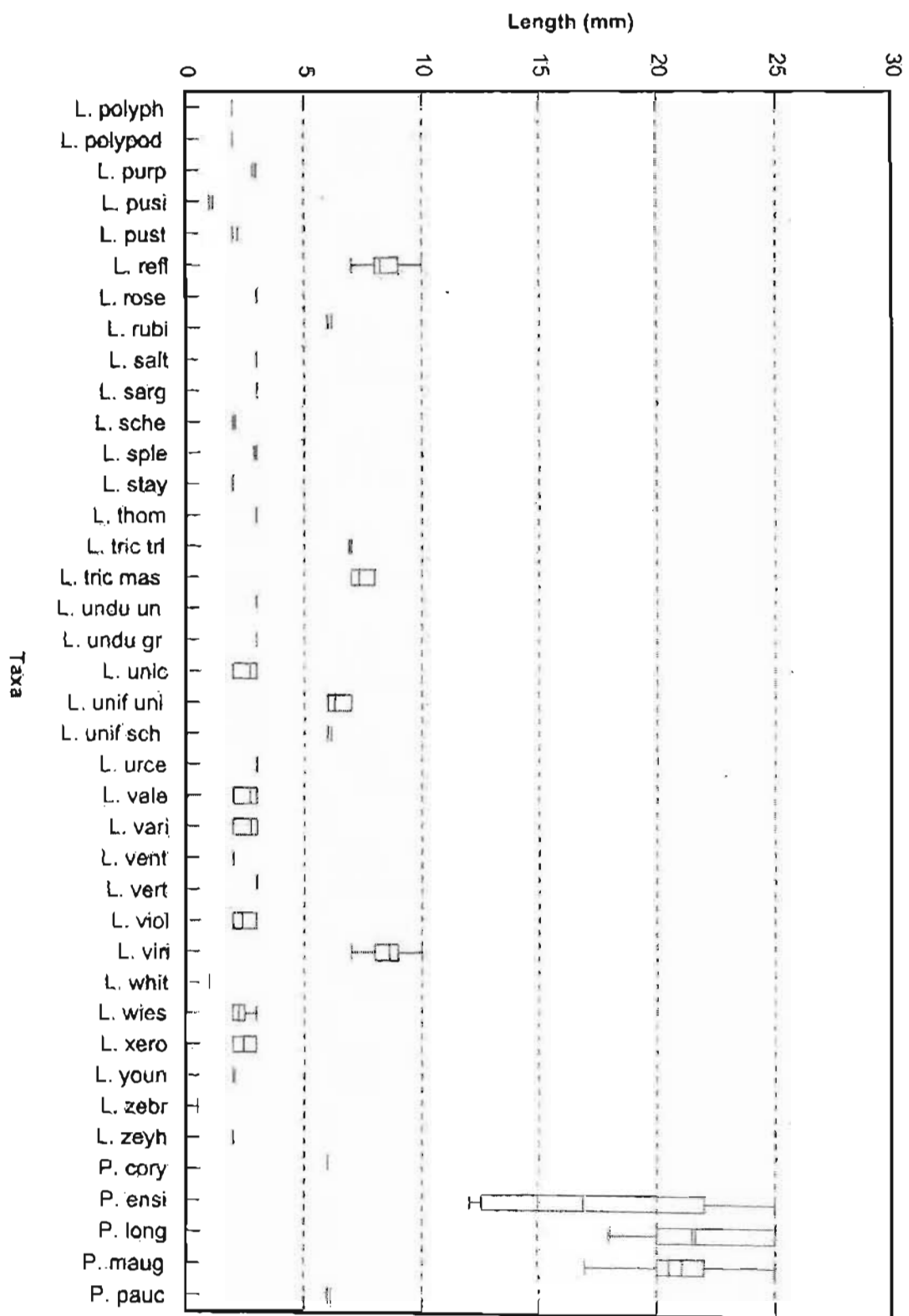


Figure 27. Perianth tube length in Lachenalia and Polyxena

Character State	Taxa
Long	<i>L. algoensis</i> , <i>L. aloides</i> (all eight varieties), <i>L. bulbifera</i> , <i>L. marginata</i> subsp. <i>marginata</i> , <i>L. orchioides</i> (both varieties), <i>L. reflexa</i> , <i>L. rubida</i> , <i>L. trichophylla</i> (both subspecies), <i>L. viridiflora</i> <i>P. corymbosa</i> , <i>P. ensifolia</i> , <i>P. longituba</i> , <i>P. maughanii</i> , <i>P. paucifolia</i> <i>Massonia</i>
Short	<i>L. alba</i> , <i>L. ameliae</i> , <i>L. angelica</i> , <i>L. anguinea</i> , <i>L. arbutnotiae</i> , <i>L. arida</i> , <i>L. attenuata</i> , <i>L. aurioliae</i> , <i>L. bachmannii</i> , <i>L. barkeriana</i> , <i>L. bolusii</i> , <i>L. bowkeri</i> , <i>L. buchbergensis</i> , <i>L. campanulata</i> , <i>L. canaliculata</i> , <i>L. capensis</i> , <i>L. carnosae</i> , <i>L. cernua</i> , <i>L. comptonii</i> , <i>L. concordiana</i> , <i>L. congesta</i> , <i>L. contaminata</i> (both varieties), <i>L. convallarioides</i> , <i>L. dasybotrya</i> , <i>L. dehoopensis</i> , <i>L. doleritica</i> , <i>L. duncanii</i> , <i>L. elegans</i> (all four varieties), <i>L. esterhuysenae</i> , <i>L. fasciculata</i> , <i>L. fistulosa</i> , <i>L. framesii</i> , <i>L. giessii</i> , <i>L. gillettii</i> , <i>L. glauca</i> , <i>L. glaucophylla</i> , <i>L. haarlemensis</i> , <i>L. hirta</i> (both varieties), <i>L. inconspicua</i> , <i>L. isopetala</i> , <i>L. juncifolia</i> (both varieties), <i>L. karooica</i> , <i>L. klinghardtiana</i> , <i>L. kliprandensis</i> , <i>L. komsbergensis</i> , <i>L. lactosa</i> , <i>L. latimerae</i> , <i>L. leipoldtii</i> , <i>L. leomontana</i> , <i>L. liliiflora</i> , <i>L. longibracteata</i> , <i>L. lutea</i> , <i>L. macgregoriorum</i> , <i>L. margaretae</i> , <i>L. marginata</i> , subsp. <i>neglecta</i> , <i>L. marlothii</i> , <i>L. martinae</i> , <i>L. mathewsii</i> , <i>L. maximiliani</i> , <i>L. mediana</i> (both varieties), <i>L. minima</i> , <i>L. moniliformis</i> , <i>L. montana</i> , <i>L. muiirii</i> , <i>L. multifolia</i> , <i>L. mutabilis</i> , <i>L. namaquensis</i> , <i>L. namibiensis</i> , <i>L. nardouwensis</i> , <i>L. neilii</i> , <i>L. nervosa</i> , <i>L. nordenstamii</i> , <i>L. mutans</i> , <i>L. obscura</i> , <i>L. orthopetala</i> , <i>L. patula</i> , <i>L. pearsonii</i> , <i>L. peersii</i> , <i>L. perryae</i> , <i>L. physocaulos</i> , <i>L. polyphylla</i> , <i>L. polypodantha</i> , <i>L. purpureocaerulea</i> , <i>L. pusilla</i> , <i>L. pustulata</i> , <i>L. rosea</i> , <i>L. salteri</i> , <i>L. sargeantii</i> , <i>L. schelpei</i> , <i>L. splendida</i> , <i>L. stayneri</i> , <i>L. thomasiae</i> , <i>L. undulata</i> (both subspecies), <i>L. unicolor</i> , <i>L. unifolia</i> (both varieties), <i>L. urceolata</i> , <i>L. valeriae</i> , <i>L. variegata</i> , <i>L. ventricosa</i> , <i>L. verticillata</i> , <i>L. violacea</i> , <i>L. whitehillensis</i> , <i>L. wiesei</i> , <i>L. xerophila</i> , <i>L. youngii</i> , <i>L. zebrina</i> , <i>L. zeyheri</i>

3) **Perianth tube shape.** Three states occurred: tubular (=0); cup-shaped (=1); and disc-shaped (=2). Qualitative character, scored as character 40 (Appendix 1).

Tubular perianth tubes occurred in *Massonia* and 23 (16.5%) ingroup taxa (18 *Lachenalia*, all five *Polyxena*) (Figures 23A, 25A). Cup-shaped perianth tubes occurred in 115 (83%) *Lachenalia* taxa (Figure 25B-E), and disc-shaped perianth tubes only occurred in *L. zebrina* (Table 29).

Character State	Taxa
Tubular	<i>L. algoensis</i> , <i>L. aloides</i> (all eight varieties), <i>L. bulbifera</i> , <i>L. marginata</i> subsp. <i>marginata</i> , <i>L. orchioides</i> (both varieties), <i>L. reflexa</i> , <i>L. rubida</i> , <i>L. trichophylla</i> (both subspecies), <i>L. viridiflora</i> <i>P. corymbosa</i> , <i>P. ensifolia</i> , <i>P. longituba</i> , <i>P. maughanii</i> , <i>P. paucifolia</i> <i>Massonia</i>
Cup-shaped	<i>L. alba</i> , <i>L. ameliae</i> , <i>L. angelica</i> , <i>L. anguinea</i> , <i>L. arbutnotiae</i> , <i>L. arida</i> , <i>L. attenuata</i> , <i>L. aurioliae</i> , <i>L. bachmannii</i> , <i>L. barkeriana</i> , <i>L. bolusii</i> , <i>L. bowkeri</i> , <i>L. buchbergensis</i> , <i>L. campanulata</i> , <i>L. canaliculata</i> , <i>L. capensis</i> , <i>L. carnosa</i> , <i>L. cernua</i> , <i>L. comptonii</i> , <i>L. concordiana</i> , <i>L. congesta</i> , <i>L. contaminata</i> (both varieties), <i>L. corvalliarioides</i> , <i>L. dasybotrya</i> , <i>L. dehoopensis</i> , <i>L. doleritica</i> , <i>L. duncanii</i> , <i>L. elegans</i> (all four varieties), <i>L. esterhuysenae</i> , <i>L. fasciculata</i> , <i>L. fistulosa</i> , <i>L. framesii</i> , <i>L. giessii</i> , <i>L. gillettii</i> , <i>L. glauca</i> , <i>L. glaucophylla</i> , <i>L. haarlemensis</i> , <i>L. hirta</i> (both varieties), <i>L. inconspicua</i> , <i>L. isopetala</i> , <i>L. juncifolia</i> (both varieties), <i>L. karooica</i> , <i>L. klinghardtiana</i> , <i>L. kliprandensis</i> , <i>L. komsbergensis</i> , <i>L. lactosa</i> , <i>L. latimerae</i> , <i>L. leipoldtii</i> , <i>L. leomontana</i> , <i>L. liliiflora</i> , <i>L. longibracteata</i> , <i>L. lutea</i> , <i>L. macgregorium</i> , <i>L. margaretae</i> , <i>L. marginata</i> subsp. <i>neglecta</i> , <i>L. marlothii</i> , <i>L. martiniae</i> , <i>L. mathewsii</i> , <i>L. maximiliani</i> , <i>L. mediana</i> (both varieties), <i>L. minima</i> , <i>L. moniliformis</i> , <i>L. montana</i> , <i>L. muirii</i> , <i>L. multifolia</i> , <i>L. mutabilis</i> , <i>L. namaquensis</i> , <i>L. namibiensis</i> , <i>L. nardourwensis</i> , <i>L. neilii</i> , <i>L. nervosa</i> , <i>L. nordenstamii</i> , <i>L. nutans</i> , <i>L. obscura</i> , <i>L. orthopetala</i> , <i>L. patula</i> , <i>L. pearsonii</i> , <i>L. peersii</i> , <i>L. perryae</i> , <i>L. physocaulos</i> , <i>L. polyphylla</i> , <i>L. polypodantha</i> , <i>L. purpleocaerulea</i> , <i>L. pusilla</i> , <i>L. pustulata</i> , <i>L. rosea</i> , <i>L. salteri</i> , <i>L. sargeantii</i> , <i>L. schelpei</i> , <i>L. splendida</i> , <i>L. stayneri</i> , <i>L. thomasiae</i> , <i>L. undulata</i> (both subspecies), <i>L. unicolor</i> , <i>L. unifolia</i> (both varieties) <i>L. urceolata</i> , <i>L. valeriae</i> , <i>L. variegata</i> , <i>L. ventricosa</i> , <i>L. verticillata</i> , <i>L. violacea</i> , <i>L. whitehillensis</i> , <i>L. wieseii</i> , <i>L. xerophila</i> , <i>L. youngii</i> , <i>L. zeyheri</i>
Disc-shaped	<i>L. zebrina</i>

4) **Flower arrangement.** Two states occurred: spiral (=0); and three-flowered whorls (=1). Qualitative character, scored as character 41 (Appendix 1).

Flowers were spirally arranged in *Massonia*, all five *Polyxena* taxa, and in 125 (90%) *Lachenalia* taxa (Figure 25A-E). In 14 (10 %) *Lachenalia* taxa the flowers were arranged in discrete three-flowered whorls (*L. aurioliae*, *L. canaliculata*, *L. concordiana*, *L. elegans* var. *flava*, *L. elegans* var. *membranacea*, *L. elegans* var. *suaveolens*, *L. fasciculata*, *L. inconspicua*, *L. marlothii*, *L. obscura*, *L. trichophylla* subsp. *trichophylla*, *L. urceolata*, *L. verticillata* (Figure 22C) and *L. wieseii*).

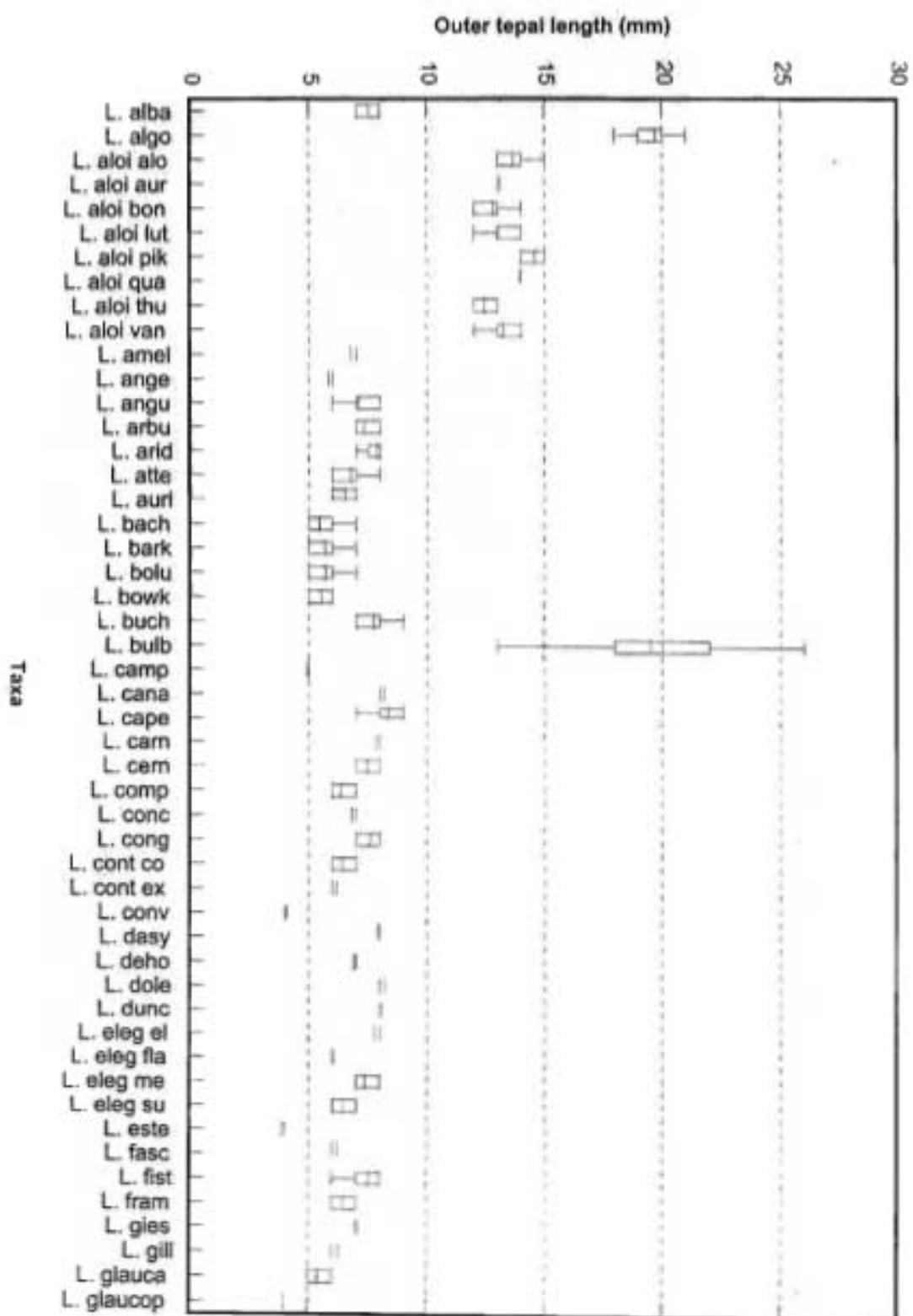
5) **Outer tepal shape.** Two states occurred: oblong (=0); and ovate (=1). Qualitative character, scored as character 42 (Appendix 1).

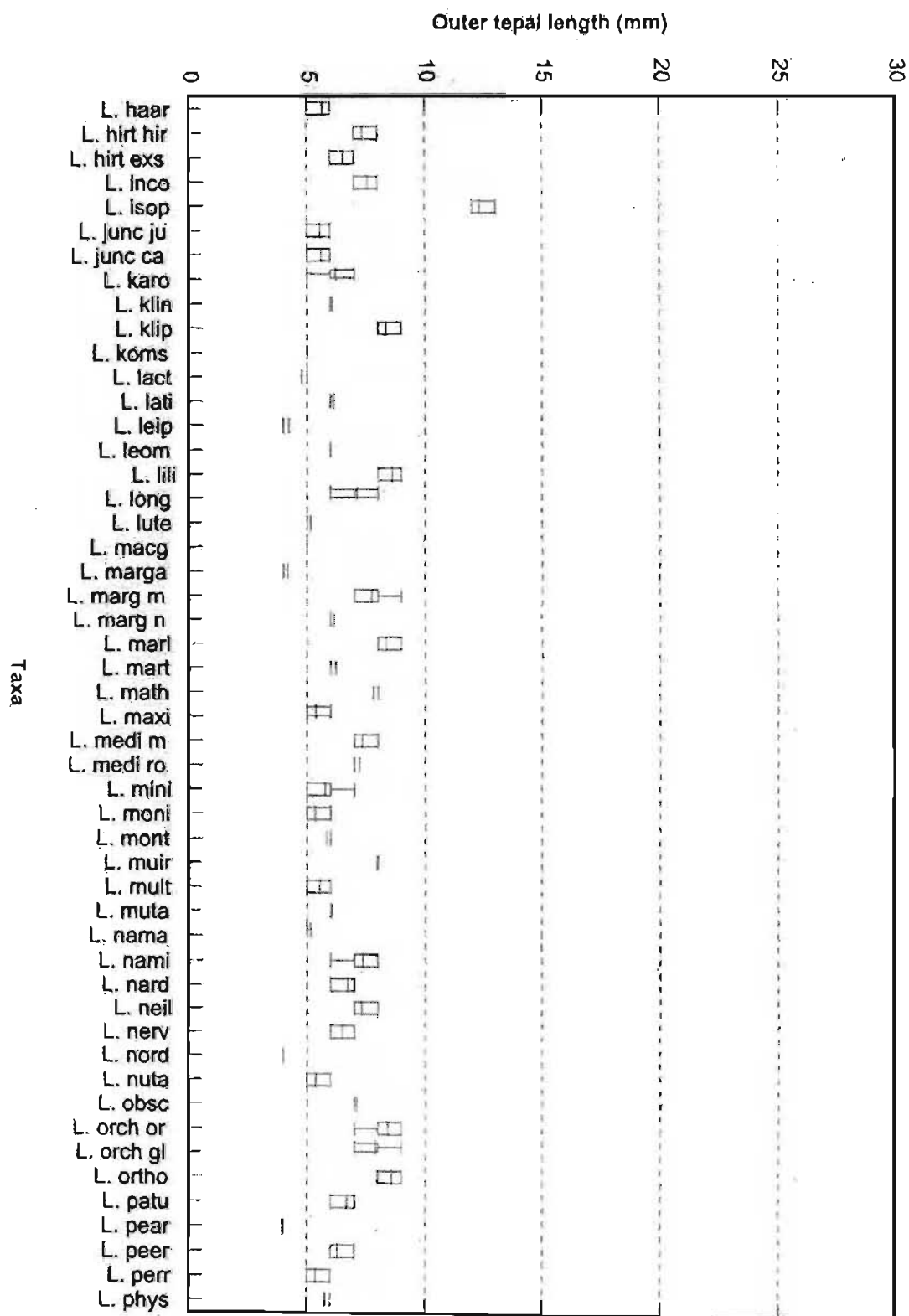
Oblong outer tepals with nearly parallel sides occurred in *Massonia*. This tepal form also occurred in 17 (14%) ingroup species (12 *Lachenalia*, all five *Polyxena*). In 103 (86%) *Lachenalia* species, outer tepals were ovate and scarcely twice as long as broad (Table 30).

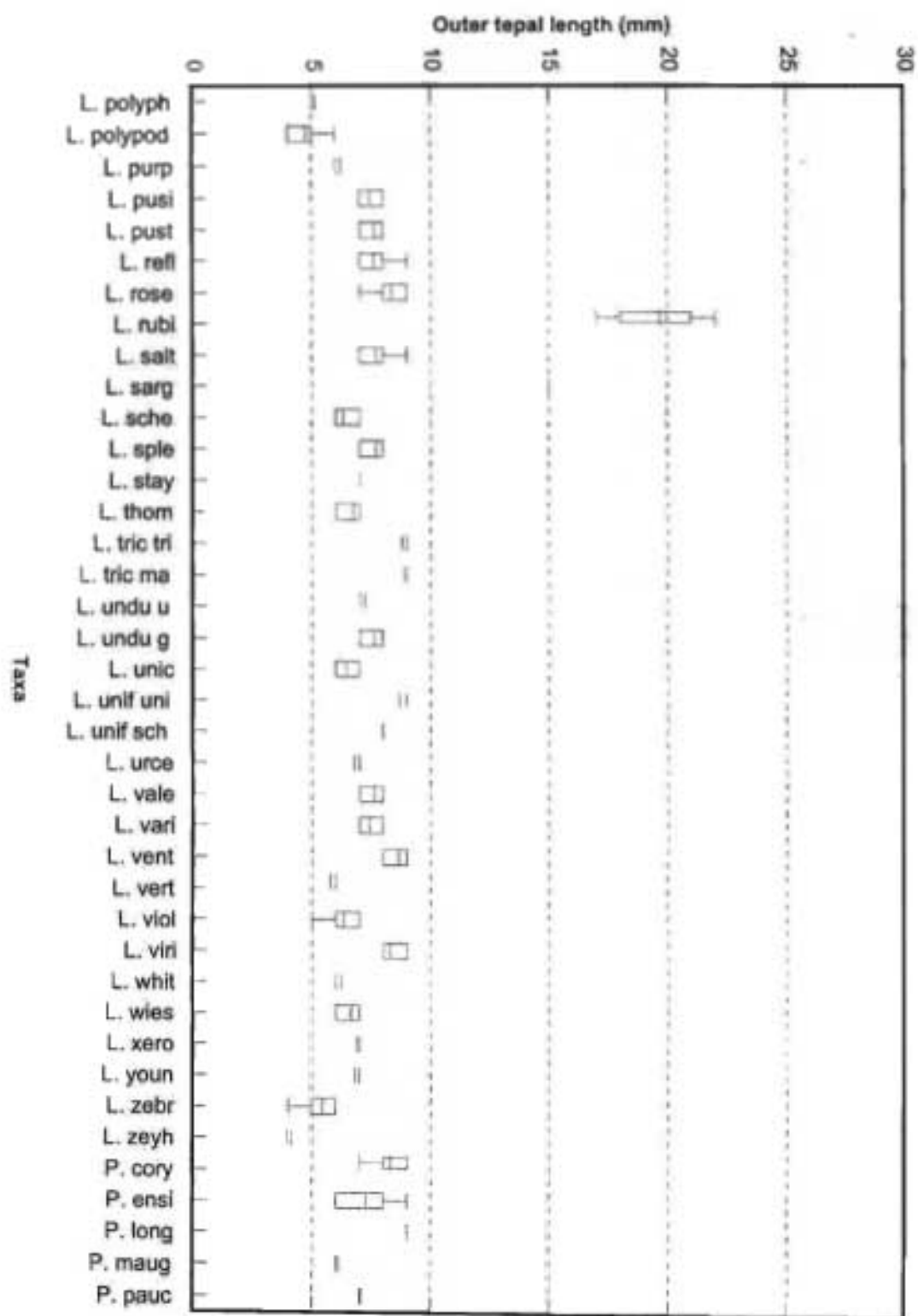
Character State	Species
Oblong	<i>L. algoensis</i> , <i>L. aloides</i> (all eight varieties), <i>L. barkeriana</i> , <i>L. bulbifera</i> , <i>L. isopetala</i> , <i>L. pusilla</i> , <i>L. reflexa</i> , <i>L. rubida</i> , <i>L. sargeantii</i> , <i>L. trichophylla</i> (both subspecies), <i>L. unifolia</i> (both varieties), <i>L. viridiflora</i> <i>P. corymbosa</i> , <i>P. ensifolia</i> , <i>P. longituba</i> , <i>P. maughanii</i> , <i>P. paucifolia</i> <i>Massonia</i>
Ovate	<i>L. alba</i> , <i>L. ameliae</i> , <i>L. angelica</i> , <i>L. anguinea</i> , <i>L. arbutnotiae</i> , <i>L. arida</i> , <i>L. attenuata</i> , <i>L. aurioliae</i> , <i>L. bachmannii</i> , <i>L. bolusii</i> , <i>L. bowkeri</i> , <i>L. buchbergensis</i> , <i>L. campanulata</i> , <i>L. canaliculata</i> , <i>L. capensis</i> , <i>L. carnosa</i> , <i>L. cernua</i> , <i>L. comptonii</i> , <i>L. concordiana</i> , <i>L. congesta</i> , <i>L. contaminata</i> (both varieties), <i>L. convallarioides</i> , <i>L. dasybotrya</i> , <i>L. dehoopensis</i> , <i>L. doleritica</i> , <i>L. duncanii</i> , <i>L. elegans</i> (all four varieties), <i>L. esterhuysenae</i> , <i>L. fasciculata</i> , <i>L. fistulosa</i> , <i>L. framesii</i> , <i>L. giessii</i> , <i>L. gillettii</i> , <i>L. glauca</i> , <i>L. glaucophylla</i> , <i>L. haarlemensis</i> , <i>L. hirta</i> (both varieties), <i>L. inconspicua</i> , <i>L. juncifolia</i> (both varieties), <i>L. karooica</i> , <i>L. klinghardtiana</i> , <i>L. kliprandensis</i> , <i>L. komsbergensis</i> , <i>L. lactosa</i> , <i>L. latimerae</i> , <i>L. leipoldtii</i> , <i>L. leomontana</i> , <i>L. liliiflora</i> , <i>L. longibracteata</i> , <i>L. lutea</i> , <i>L. macgregoriorum</i> , <i>L. margaretae</i> , <i>L. marginata</i> (both subspecies), <i>L. marlothii</i> , <i>L. martinae</i> , <i>L. mathewsii</i> , <i>L. maximiliani</i> , <i>L. mediana</i> (both varieties), <i>L. minima</i> , <i>L. moniliformis</i> , <i>L. montana</i> , <i>L. muirii</i> , <i>L. multifolia</i> , <i>L. mutabilis</i> , <i>L. namaquensis</i> , <i>L. namibiensis</i> , <i>L. nardouwensis</i> , <i>L. neilii</i> , <i>L. nervosa</i> , <i>L. nordenstamii</i> , <i>L. nutans</i> , <i>L. obscura</i> , <i>L. orchiioides</i> (both varieties), <i>L. orthopetala</i> , <i>L. patula</i> , <i>L. pearsonii</i> , <i>L. peersii</i> , <i>L. perryae</i> , <i>L. physocaulos</i> , <i>L. polyphylla</i> , <i>L. polypodantha</i> , <i>L. purpureocaerulea</i> , <i>L. pustulata</i> , <i>L. rosea</i> , <i>L. salteri</i> , <i>L. schelpei</i> , <i>L. splendida</i> , <i>L. stayneri</i> , <i>L. thomasiae</i> , <i>L. undulata</i> (both subspecies), <i>L. unicolor</i> , <i>L. urceolata</i> , <i>L. valeriae</i> , <i>L. variegata</i> , <i>L. ventricosa</i> , <i>L. verticillata</i> , <i>L. violacea</i> , <i>L. whitehillensis</i> , <i>L. wiesei</i> , <i>L. xerophila</i> , <i>L. youngii</i> , <i>L. zebrina</i> , <i>L. zeyheri</i>

6) **Outer tepal length.** Two discontinuous states occurred: short tepals (=0); and long tepals (=1). Quantitative character, scored as character 43 (Appendix 1).

Short outer tepals occurred in *Massonia* and 114 (95%) ingroup species (109 *Lachenalia*, all five *Polyxena*) in which the tepals were up to 9 mm long (Figure 25B-E). Long outer tepals occurred on six (5%) *Lachenalia* species in which the tepals were 12 mm long or longer (*L. algoensis*, *L. aloides* (all eight varieties) (Figure 25A), *L. bulbifera*, *L. isopetala*, *L. rubida* and *L. sargeantii*) (Figure 28).

Figure 28. Outer tepal length in *Lachenalia* and *Polyxena*

Figure 28. Outer tepal length in *Lachenalia* and *Polyxena*

Figure 28. Outer tepal length in *Lachenalia* and *Polyxena*

7) **Outer tepal apex.** Two states occurred: recurved apices (=0); and flat apices (=1). Qualitative character, scored as character 44 (Appendix 1).

Recurved outer tepal apices occurred in *Massonia* and in 15 (12.5%) ingroup species (*L. ameliae*, *L. angelica*, *L. campanulata*, *L. comptonii*, *L. congesta*, *L. glaucophylla*, *L. minima*, *L. multifolia*, *L. nervosa*, *L. nordenstamii*, all five *Polyxena*). Flat tepal apices occurred in 105 (87.5%) *Lachenalia* species.

Inner tepal apices were slightly flared in most species but in others they were moderately to distinctly recurved, or straight, but did not form clearly discontinuous classes. Both inner and outer tepal margins were flat in most species but in some they were more or less undulate, as in *L. fistulosa*.

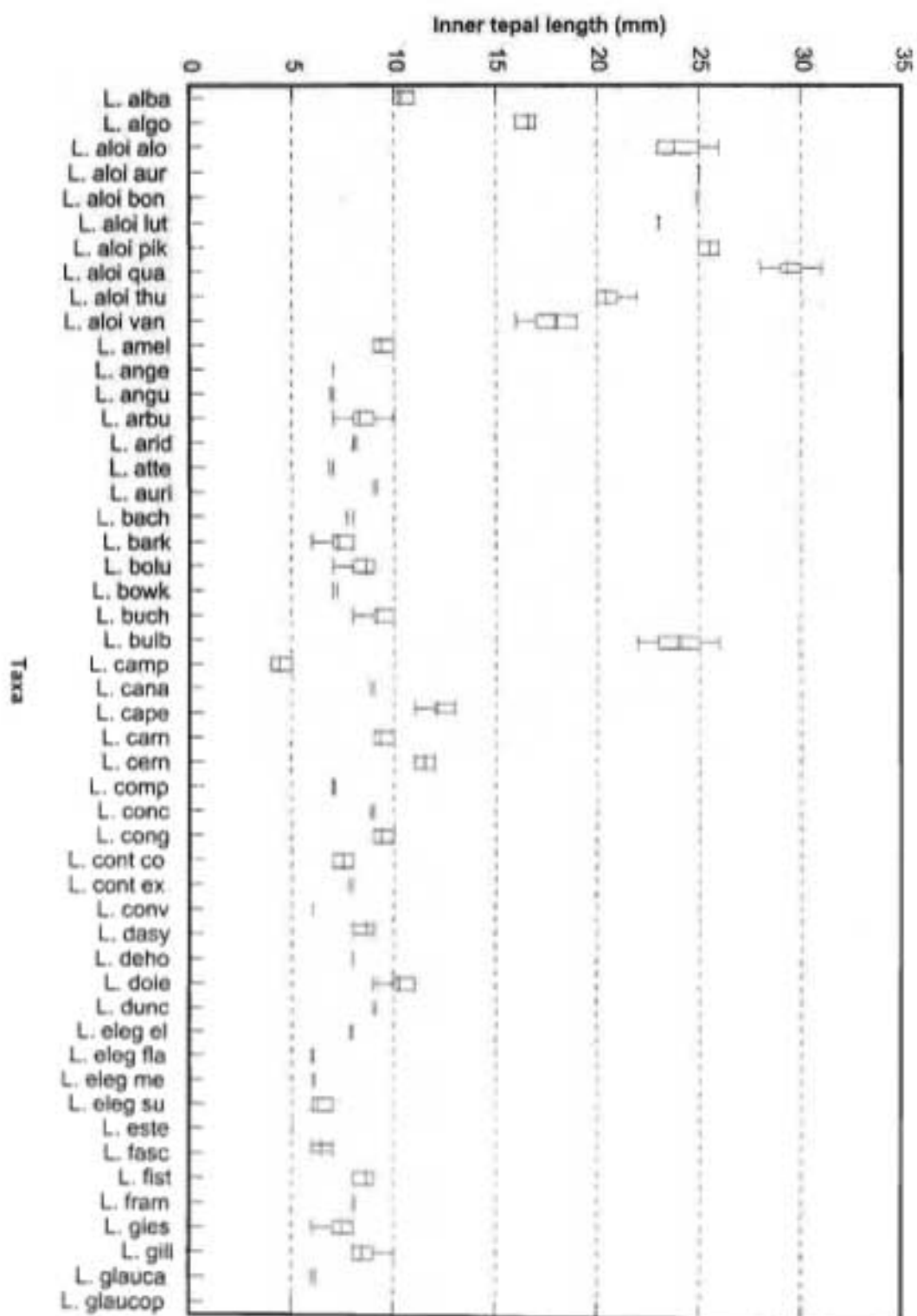
8) **Inner tepal shape.** Three states occurred: linear-oblong (=0); obovate (=1); and oblong-obovate (=2). Qualitative character, scored as character 45 (Appendix 1).

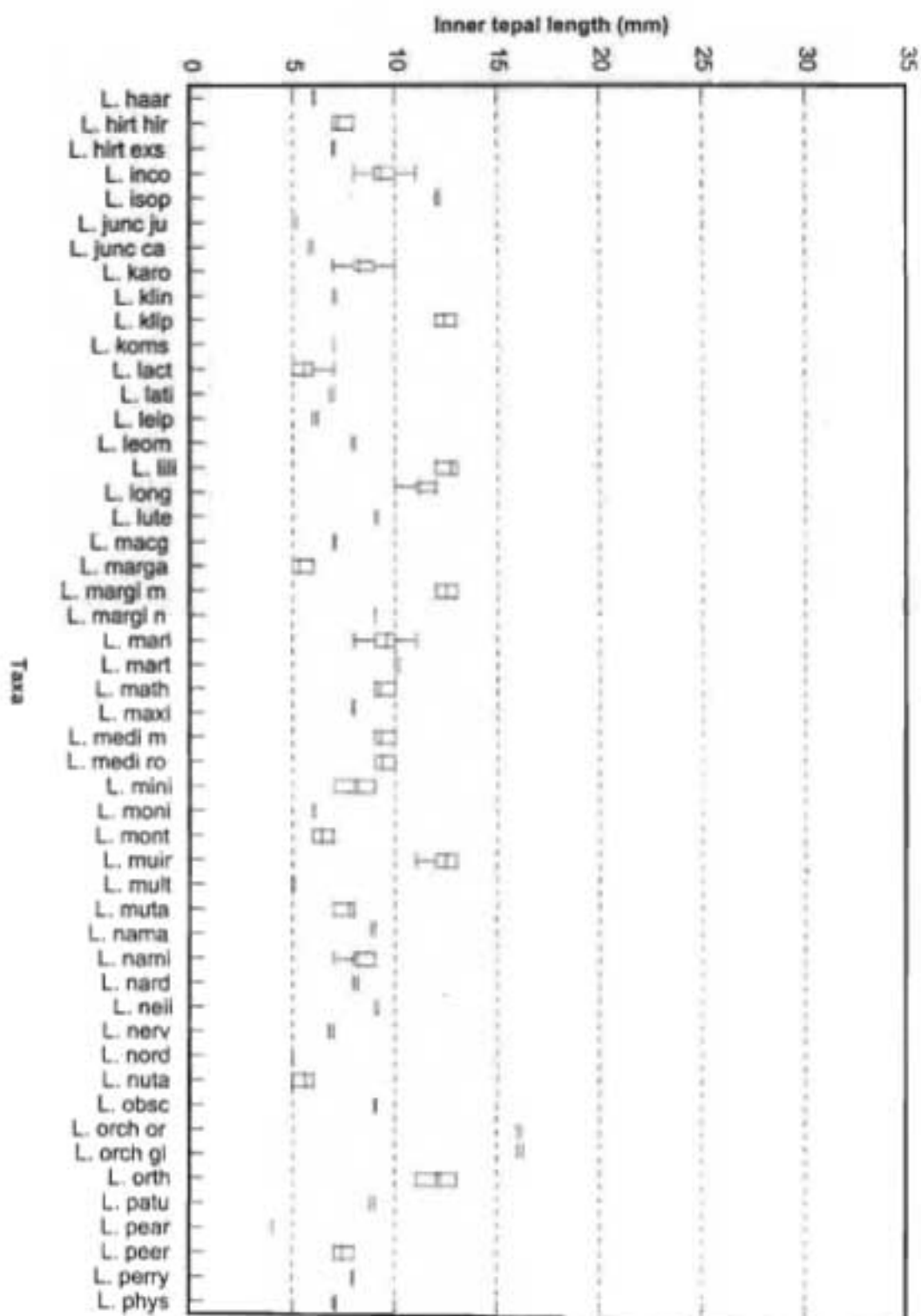
Linear-oblong inner tepals occurred in *Massonia* and in 21 (17.5%) ingroup species (16 *Lachenalia*, all five *Polyxena*). In 93 (77.5 %) *Lachenalia* species the inner tepals were obovate and in six (5%) *Lachenalia* species they were oblong-obovate (Table 31).

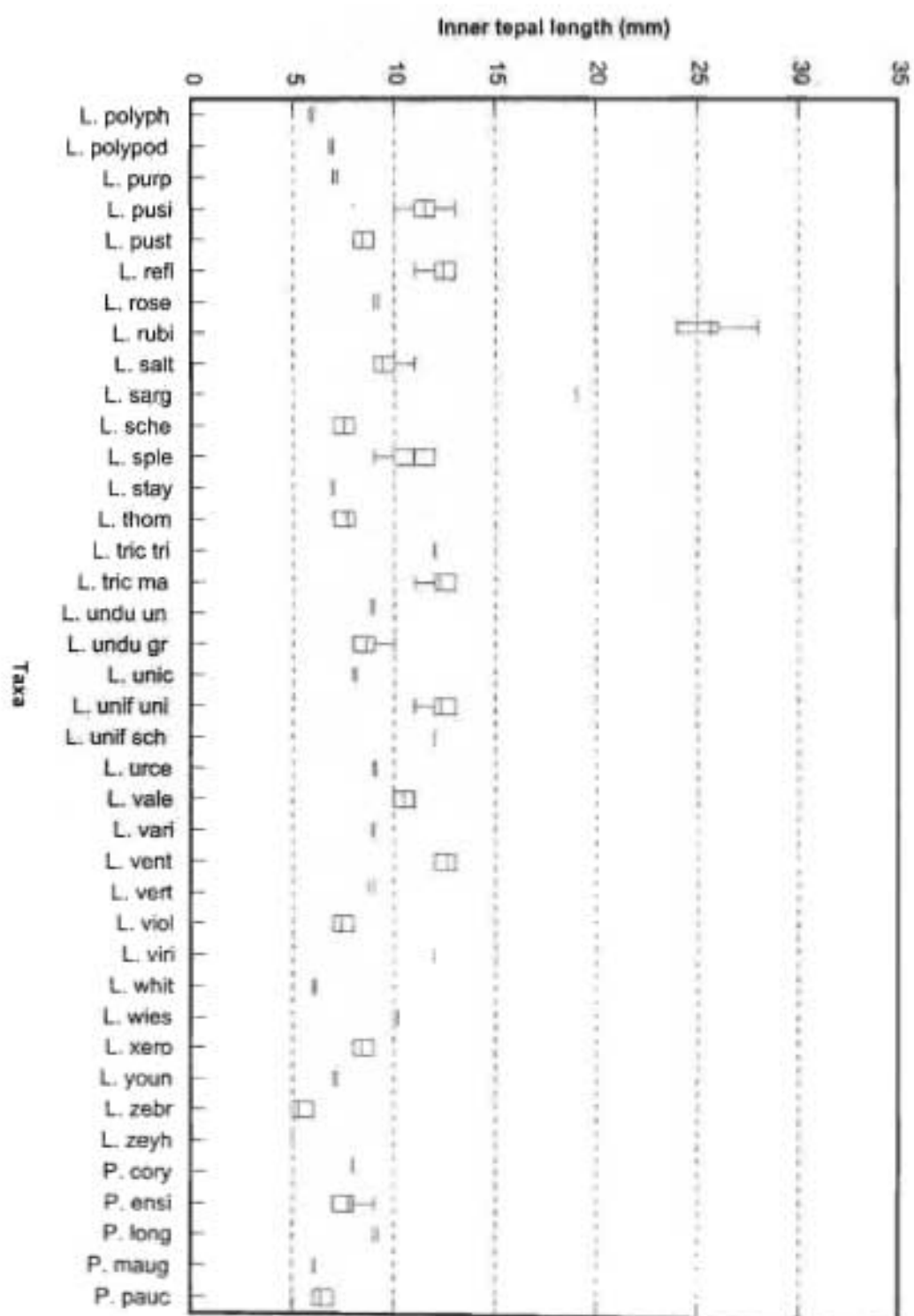
Table 31. Variation in inner tepal shape in <i>Lachenalia</i> , <i>Polyxena</i> and the outgroup <i>Massonia</i>	
Character State	Species
Linear-oblong	<i>L. arida</i> , <i>L. barkeriana</i> , <i>L. campanulata</i> , <i>L. comptonii</i> , <i>L. contaminata</i> (both varieties), <i>L. giessii</i> , <i>L. glaucophylla</i> , <i>L. isopetala</i> , <i>L. macgregoriorum</i> , <i>L. muirii</i> , <i>L. multifolia</i> , <i>L. namibiensis</i> , <i>L. nervosa</i> , <i>L. nordenstamii</i> , <i>L. pearsonii</i> , <i>L. pusilla</i> <i>P. corymbosa</i> , <i>P. ensifolia</i> , <i>P. longituba</i> , <i>P. maughanii</i> , <i>P. paucifolia</i> <i>Massonia</i>
Obovate	<i>L. alba</i> , <i>L. ameliae</i> , <i>L. angelica</i> , <i>L. anguinea</i> , <i>L. arbutnotiae</i> , <i>L. attenuata</i> , <i>L. aurioliae</i> , <i>L. bachmannii</i> , <i>L. bolusii</i> , <i>L. bowkeri</i> , <i>L. buchbergensis</i> , <i>L. canaliculata</i> , <i>L. capensis</i> , <i>L. carnosae</i> , <i>L. cernua</i> , <i>L. concordiana</i> , <i>L. congesta</i> , <i>L. convallarioides</i> , <i>L. dasybotrya</i> , <i>L. dehoopensis</i> , <i>L. doleritica</i> , <i>L. duncanii</i> , <i>L. elegans</i> (all four varieties), <i>L. esterhuysenae</i> , <i>L. fasciculata</i> , <i>L. fistulosa</i> , <i>L. framesii</i> , <i>L. gillettii</i> , <i>L. glauca</i> , <i>L. haarlemensis</i> , <i>L. hirta</i> (both varieties), <i>L. inconspicua</i> , <i>L. juncifolia</i> (both varieties), <i>L. karooica</i> , <i>L. klinghardtiana</i> , <i>L. kliprandensis</i> , <i>L. komsbergensis</i> , <i>L. lactosa</i> , <i>L. latimeriae</i> , <i>L. leipoldtii</i> , <i>L. leomontana</i> , <i>L. liliiflora</i> , <i>L. longibracteata</i> , <i>L. lutea</i> , <i>L. margaretae</i> , <i>L. marginata</i> (both subspecies), <i>L. marlothii</i> , <i>L. martinae</i> , <i>L. mathewsii</i> , <i>L. maximiliani</i> , <i>L. mediana</i> (both varieties), <i>L. minima</i> , <i>L. moniliformis</i> , <i>L. montana</i> , <i>L. mutabilis</i> , <i>L. namaquensis</i> , <i>L. nardouwensis</i> , <i>L. neilii</i> , <i>L. nutans</i> , <i>L. obscura</i> , <i>L. orthopetala</i> , <i>L. patula</i> , <i>L. peersii</i> , <i>L. perryae</i> , <i>L. physocaulos</i> , <i>L. polyphylla</i> , <i>L. polypodantha</i> , <i>L. purpureocaerulea</i> , <i>L. pustulata</i> , <i>L. reflexa</i> , <i>L. rosea</i> , <i>L. salteri</i> , <i>L. schelpei</i> , <i>L. splendida</i> , <i>L. stayneri</i> , <i>L. thomasiae</i> , <i>L. trichophylla</i> (both subspecies), <i>L. undulata</i> (both subspecies), <i>L. unicolor</i> , <i>L. unifolia</i> (both varieties), <i>L. urceolata</i> , <i>L. valeriae</i> , <i>L. variegata</i> , <i>L. ventricosa</i> , <i>L. verticillata</i> , <i>L. violacea</i> , <i>L. viridiflora</i> , <i>L. whitehillensis</i> , <i>L. wiesei</i> , <i>L. xerophila</i> , <i>L. youngii</i> , <i>L. zebrina</i> , <i>L. zeyheri</i>
Oblong-obovate	<i>L. algoensis</i> , <i>L. aloides</i> (all eight varieties), <i>L. bulbifera</i> , <i>L. orchioides</i> (both varieties), <i>L. rubida</i> , <i>L. sargeantii</i>

9) **Inner tepal length.** Two discontinuous groups were defined: short tepals (=0); and long tepals (=1). Quantitative character, scored as character 46 (Appendix 1).

Massonia and 114 (95%) ingroup species (109 *Lachenalia*, all five *Polyxena*) had short inner tepals up to 13 mm long (Figure 25B-E). In six (5%) *Lachenalia* species the inner tepals were 16 mm long or longer, *L. algoensis*, *L. aloides* (all eight varieties) (Figure 25A), *L. bulbifera*, *L. orchioides* (both varieties), *L. rubida* and *L. sargeantii* (Figure 29).

Figure 29. Inner tepal length in *Lachenalia* and *Polyxena*

Figure 29. Inner tepal length in *Lachenalia* and *Polyxena*

Figure 29. Inner tepal length in *Lachenalia* and *Polyxena*

10) **Inner and outer tepal arrangement.** Two states occurred: inner and outer tepals subequal (=0), and inner tepals longer than the outer tepals (=1). Qualitative character, scored as character 47 (Appendix 1).

Subequal inner and outer tepals occurred in *Massonia* and in 46 (38%) ingroup species (41 *Lachenalia*, all five *Polyxena*) (Figure 25B, D). In 74 (62%) *Lachenalia* species the inner tepals were distinctly longer than the outer tepals (Figure 25A, C, E, Table 32).

Character state	Species
Inner and outer tepals subequal	<i>L. angelica</i> , <i>L. anguinea</i> , <i>L. arida</i> , <i>L. attenuata</i> , <i>L. buchbergensis</i> , <i>L. bulbifera</i> , <i>L. campanulata</i> , <i>L. comptonii</i> , <i>L. contaminata</i> (both varieties), <i>L. convallarioides</i> , <i>L. elegans</i> (all four varieties), <i>L. esterhuysenae</i> , <i>L. giessii</i> , <i>L. glauca</i> , <i>L. glaucophylla</i> , <i>L. hirta</i> (both varieties), <i>L. isopetala</i> , <i>L. juncifolia</i> (both varieties), <i>L. macgregoriorum</i> , <i>L. margaretae</i> , <i>L. mathewsii</i> , <i>L. maximiliani</i> , <i>L. moniliformis</i> , <i>L. multifolia</i> , <i>L. namibiensis</i> , <i>L. nardouwensis</i> , <i>L. nervosa</i> , <i>L. nordenstamii</i> , <i>L. nutans</i> , <i>L. pearsonii</i> , <i>L. polyphylla</i> , <i>L. purpureocaerulea</i> , <i>L. schelpei</i> , <i>L. stayneri</i> , <i>L. unicolor</i> , <i>L. variegata</i> , <i>L. violacea</i> , <i>L. whitehillensis</i> , <i>L. youngii</i> , <i>L. zebrina</i> , <i>L. zeyheri</i> <i>P. corymbosa</i> , <i>P. ensifolia</i> , <i>P. longituba</i> , <i>P. maughanii</i> , <i>P. paucifolia</i> <i>Massonia</i>
Inner tepals longer than outer tepals	<i>L. alba</i> , <i>L. algoensis</i> , <i>L. aloides</i> (all eight varieties), <i>L. ameliae</i> , <i>L. arbutnotiae</i> , <i>L. auriolae</i> , <i>L. bachmannii</i> , <i>L. barkeriana</i> , <i>L. bolusii</i> , <i>L. bowkeri</i> , <i>L. canaliculata</i> , <i>L. capensis</i> , <i>L. carnosae</i> , <i>L. cernua</i> , <i>L. concordiana</i> , <i>L. congesta</i> , <i>L. dasybotrya</i> , <i>L. dehoopensis</i> , <i>L. doleritica</i> , <i>L. duncanii</i> , <i>L. fasciculata</i> , <i>L. fistulosa</i> , <i>L. framesii</i> , <i>L. gillettii</i> , <i>L. haarlemensis</i> , <i>L. inconspicua</i> , <i>L. karooica</i> , <i>L. klinghardtiana</i> , <i>L. kliprandensis</i> , <i>L. komsbergensis</i> , <i>L. lactosa</i> , <i>L. latimerae</i> , <i>L. leipoldtii</i> , <i>L. leomontana</i> , <i>L. liliiflora</i> , <i>L. longibracteata</i> , <i>L. lutea</i> , <i>L. marginata</i> (both subspecies), <i>L. marlothii</i> , <i>L. martinae</i> , <i>L. mediana</i> (both varieties), <i>L. minima</i> , <i>L. montana</i> , <i>L. muiirii</i> , <i>L. mutabilis</i> , <i>L. namaquensis</i> , <i>L. neilii</i> , <i>L. obscura</i> , <i>L. orchioides</i> (both varieties), <i>L. orthopetala</i> , <i>L. patula</i> , <i>L. peersii</i> , <i>L. perryae</i> , <i>L. physocaulos</i> , <i>L. polypodantha</i> , <i>L. pusilla</i> , <i>L. pustulata</i> , <i>L. reflexa</i> , <i>L. rosea</i> , <i>L. rubida</i> , <i>L. salteri</i> , <i>L. sargeantii</i> , <i>L. splendida</i> , <i>L. thomasiae</i> , <i>L. trichophylla</i> (both subspecies), <i>L. undulata</i> (both subspecies), <i>L. unifolia</i> (both varieties), <i>L. urceolata</i> , <i>L. valeriae</i> , <i>L. ventricosa</i> , <i>L. verticillata</i> , <i>L. viridiflora</i> , <i>L. wiesei</i> , <i>L. xerophila</i>

11) **Floral symmetry.** Two states occurred: actinomorphic (=0) and zygomorphic (=1). Qualitative character, scored as character 48 (Appendix 1).

Massonia and six (5%) ingroup species (*P. corymbosa*, *P. ensifolia*, *P. longituba*, *P. maughanii*, *P. paucifolia* and *L. pearsonii*) had actinomorphic flowers (Figure 23A, B). In 114 (95%) *Lachenalia* species, floral symmetry was slightly to strongly zygomorphic (Figure 25A-E).

12) **Ventral inner tepal extension.** Three states occurred: inner tepals equal (= 0), ventral inner tepal shorter than upper inner tepals (=1), ventral inner tepal protrudes beyond upper inner tepals (=2). Qualitative character, scored as character 49 (Appendix 1).

Inner tepals of *Massonia* and 81 (67.5%) ingroup species (76 *Lachenalia*, all five *Polyxena*) were equal. In six (5%) *Lachenalia* species the ventral inner tepal was distinctly shorter than the upper inner tepals, and in 33 (27.5%) *Lachenalia* species the ventral inner tepal was distinctly longer and narrower than the upper inner tepals (Figure 25B, Table 33).

Character State	Species
Inner tepals equal	<i>L. algoensis</i> , <i>L. aloides</i> (all eight varieties), <i>L. angelica</i> , <i>L. anguinea</i> , <i>L. arbutnotiae</i> , <i>L. arida</i> , <i>L. auriolae</i> , <i>L. bachmannii</i> , <i>L. barkeriana</i> , <i>L. bowkeri</i> , <i>L. buchbergensis</i> , <i>L. campanulata</i> , <i>L. cernua</i> , <i>L. comptonii</i> , <i>L. congesta</i> , <i>L. contaminata</i> (both varieties), <i>L. convallarioides</i> , <i>L. dehoopensis</i> , <i>L. duncanii</i> , <i>L. elegans</i> (all four varieties), <i>L. esterhuysenae</i> , <i>L. fistulosa</i> , <i>L. giessii</i> , <i>L. glauca</i> , <i>L. glaucophylla</i> , <i>L. haarlemensis</i> , <i>L. isopetala</i> , <i>L. juncifolia</i> (both varieties), <i>L. karooica</i> , <i>L. komsbergensis</i> , <i>L. lactosa</i> , <i>L. latimerae</i> , <i>L. leipoldtii</i> , <i>L. leomontana</i> , <i>L. liliiflora</i> , <i>L. longibracteata</i> , <i>L. lutea</i> , <i>L. macgregorium</i> , <i>L. margaretae</i> , <i>L. minima</i> , <i>L. moniliformis</i> , <i>L. montana</i> , <i>L. muirii</i> , <i>L. multifolia</i> , <i>L. namibiensis</i> , <i>L. nardouwensis</i> , <i>L. nervosa</i> , <i>L. nordenstamii</i> , <i>L. nutans</i> , <i>L. obscura</i> , <i>L. orchioides</i> (both varieties), <i>L. orthopetala</i> , <i>L. patula</i> , <i>L. pearsonii</i> , <i>L. peersii</i> , <i>L. physocaulos</i> , <i>L. polyphylla</i> , <i>L. polypodantha</i> , <i>L. purpureocaerulea</i> , <i>L. pusilla</i> , <i>L. rosea</i> , <i>L. sargeantii</i> , <i>L. schelpei</i> , <i>L. stayneri</i> , <i>L. undulata</i> (both subspecies), <i>L. unicolor</i> , <i>L. urceolata</i> , <i>L. variegata</i> , <i>L. ventricosa</i> , <i>L. violacea</i> , <i>L. whitehillensis</i> , <i>L. wiesei</i> , <i>L. xerophila</i> , <i>L. youngii</i> , <i>L. zebrina</i> , <i>L. zeyheri</i> <i>P. corymbosa</i> , <i>P. ensifolia</i> , <i>P. longituba</i> , <i>P. maughanii</i> , <i>P. paucifolia</i> <i>Massonia</i>
Ventral inner tepal shorter than upper inner tepals	<i>L. bulbifera</i> , <i>L. capensis</i> , <i>L. martinae</i> , <i>L. reflexa</i> , <i>L. rubida</i> , <i>L. viridiflora</i>
Ventral inner tepal protrudes beyond upper inner tepals	<i>L. alba</i> , <i>L. ameliae</i> , <i>L. attenuata</i> , <i>L. bolusii</i> , <i>L. canaliculata</i> , <i>L. carnosa</i> , <i>L. concordiana</i> , <i>L. dasybotrya</i> , <i>L. doleritica</i> , <i>L. fasciculata</i> , <i>L. framesii</i> , <i>L. gillettii</i> , <i>L. hirta</i> (both varieties), <i>L. inconspicua</i> , <i>L. klinghardtiana</i> , <i>L. kliprandensis</i> , <i>L. marginata</i> (both subspecies), <i>L. marlothii</i> , <i>L. mathewsii</i> , <i>L. maximiliani</i> , <i>L. mediana</i> (both varieties), <i>L. mutabilis</i> , <i>L. namaquensis</i> , <i>L. neilii</i> , <i>L. perryae</i> , <i>L. pustulata</i> , <i>L. salteri</i> , <i>L. splendida</i> , <i>L. thomasiae</i> , <i>L. trichophylla</i> (both subspecies), <i>L. unifolia</i> (both varieties), <i>L. valeriae</i> , <i>L. verticillata</i>

5.14 FLOWER PIGMENTS

Colour is of vital importance to most flowers since it attracts pollinators, without which seed production may not occur. Floral pigments are synthesized by complex chemical processes within the cells, with each step in the biosynthetic pathway controlled by a different enzyme (Vogelpoel 1986). Pigments are synthesized in plastids or in the cytoplasm. Plastid pigments are regulated, in part, by maternally inherited DNA. By contrast, anthocyanin production is regulated by sexually inherited genes. Plastid and/or anthocyanin pigments are present in various regions of the inner and outer tepals of all species of *Lachenalia* and *Polyxena* and combine to form a wide range of colours. Flowers having the structural colour white have a

colourless epidermis and are not the product of anthocyanins. The white effect is a product of light reflected by aerenchymatous (non-pigmented) tissues (Fox 1979).

5.14.1 Materials and methods

Fresh inner and outer tepals were collected across the full range of colour forms present in *Lachenalia* and *Polyxena*. Transverse hand sections were mounted in water on microscope slides and viewed using a Zeiss light microscope.

5.14.2 Results

5.14.2.1 Plastid Pigments

Plastids contain oil soluble pigments, and are under the dominant control of genes within the cell nucleus (Vogelpoel 1995). In *Lachenalia* and *Polyxena*, plastid pigments occurred in chloroplasts and chromoplasts in the mesophyll tissue and were always absent from the epidermis. They were present in both the inner and outer tepals, where they occurred throughout the mesophyll, or were completely absent from some cells. Plastids occurred with anthocyanin pigments in the same cells of the mesophyll in some species, or they occurred separately. The plastid pigments of *Lachenalia* flowers were orange, yellow and green, and in *Polyxena*, only green. Chlorophyll was the most common pigment and was present in the flowers of most *Lachenalia* species.

Xanthophylls occurred in relatively few species with pale yellow flowers and carotenoids occurred in flowers which were bright yellowish-orange or orange, where they were found in chromoplasts throughout the mesophyll, but were concentrated in the outermost three or four layers of the tepals, and were overlain by a colourless epidermis.

Chlorophyll occurred mainly in the gibbositities of the outer tepals, and in the keels of the

inner and outer tepals of *Lachenalia* species and *Polyxena ensifolia* (Appendix 3).

5.14.2.2 Anthocyanin Pigments

In most angiosperm families, water-soluble anthocyanin pigments occur within the vacuoles of epidermal cells (Kay *et al.* 1981, Vogelpoel 1995), but in most *Lachenalia* and in all *Polyxena* species, they occurred in vacuoles in the tepal mesophyll. Anthocyanin pigments did occur in the epidermis of three taxa, in the purple flowertips of the inner tepals of *L. aloides* var. *bonaspei* and *L. aloides* var. *quadricolor*, and in the turquoise inner and outer tepals of *L. viridiflora*. In most species anthocyanins were restricted to the outer mesophyll, but in some species like *L. patula* and *L. youngii*, they were also present in the innermost cell layer. In certain varieties of *L. aloides*, anthocyanins were restricted to the outermost mesophyll layer, in the red portion of the outer tepals, where the outermost layer contained magenta anthocyanin. Here they overlay several layers of mesophyll containing carotenoid pigment present in chromoplasts. Where outer and/or inner tepals were suffused with different colours close together such as blue and pink in *L. salteri*, the different coloured pigments occurred in discrete areas (Appendix 3).

The colours of anthocyanin pigments in *Lachenalia* and *Polyxena* flowers were blue, pink, purple and magenta, with magenta being the predominant colour.

5.15 STAMENS

5.15.1 Results

The stamens of *Lachenalia* and *Polyxena* were biseriate to a greater or lesser degree. Filaments were variously inserted from the base to the mouth of the perianth tube. The distance between the two levels of insertion was greater in species with long tubular flowers. The outer stamen series was inserted at a lower level than the inner series. The anthers of the outer series opened about 24 hours before the inner series. Degree of stamen exertion

among *L. contaminata* and *L. hirta* varied considerably; most forms had included or slightly exerted stamens but both species included forms with well exerted stamens.

Filaments were terete and slender in all species of the two genera, with the width more or less stable except in *L. barkeriana*, where the upper portion was distinctly swollen, and in *L. nordenstamii*, where the filaments were relatively stout. Filament apices were acute in all species.

Filament length varied from 1 mm (*P. paucifolia*) to 33 mm (*L. bulbifera*) and was variable within species. In relation to the length of the style, filaments were shorter than the style, equal to the style, or longer than the style; in most species, filaments were longer than the style.

The anthers of the long-tubed species of *Lachenalia* were basifixed, as in *L. aloides* (Figures 30 A, 31 A,B), whereas in all other species of this genus as well as in *Polyxena*, they were attached more or less dorsifixed (Figure 30 B-D). The anthers in all members of *Lachenalia* and *Polyxena* were oblong and of fairly consistent size 1.0 x 0.5 mm, but for taxa with large tubular flowers such as *L. aloides* and *L. bulbifera* anther size increased to 2.5 x 1.0 mm. Anthers were epipeltate, versatile and dehisced longitudinally (Figure 31 B). Anther colour varied from dark green, blue, purple brown, maroon or dull red prior to anthesis, and from pale to bright yellow during anthesis. Following anthesis, the anthers remained yellow in most species, but those of three species turned black (*L. convallarioides*, *L. esterhuysenae* and *L. juncifolia*). In relation to the length of the perianth, the anthers were either included within the perianth (shorter than the perianth), or shortly to well exerted beyond the perianth. The species with the most exerted stamens were *L. barkeriana* and *L. pusilla* (Figure 22F), which were exerted up to 10 mm beyond the tip of the perianth. Filament orientation is probably pollinator-driven.

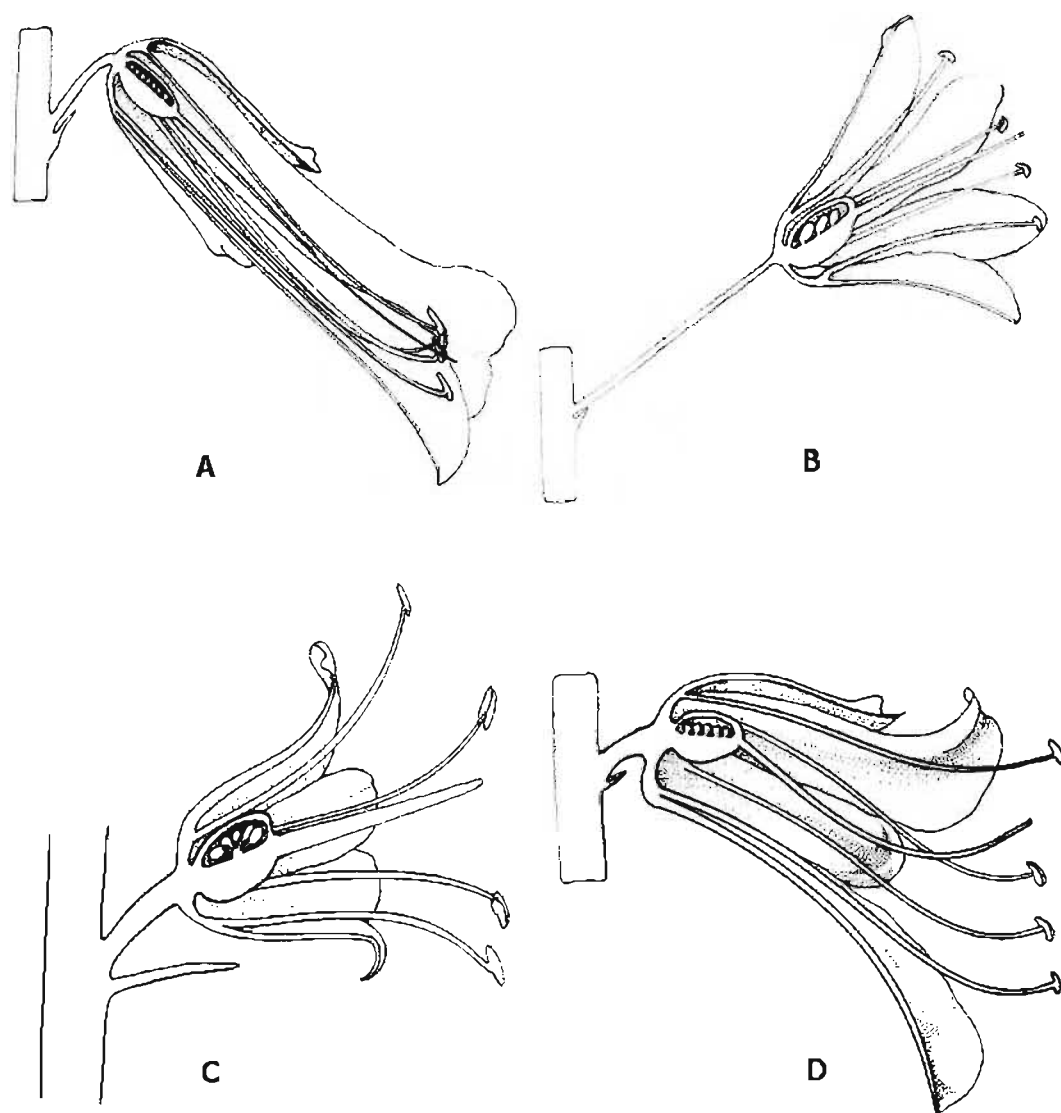


Figure 30. Variation in filament orientation in *Lachenalia*.

A, straight filaments of *L. aloides* var. *aurea* (Duncan 363) X4;

B, narrowly spreading filaments of *L. giessii* (Lavranos 19917) X4;

C, recurved filaments of *L. nervosa* (Thomas s.n.) X4;

D, declinate filaments of *L. mediana* var. *mediana* (Duncan 209) X4.

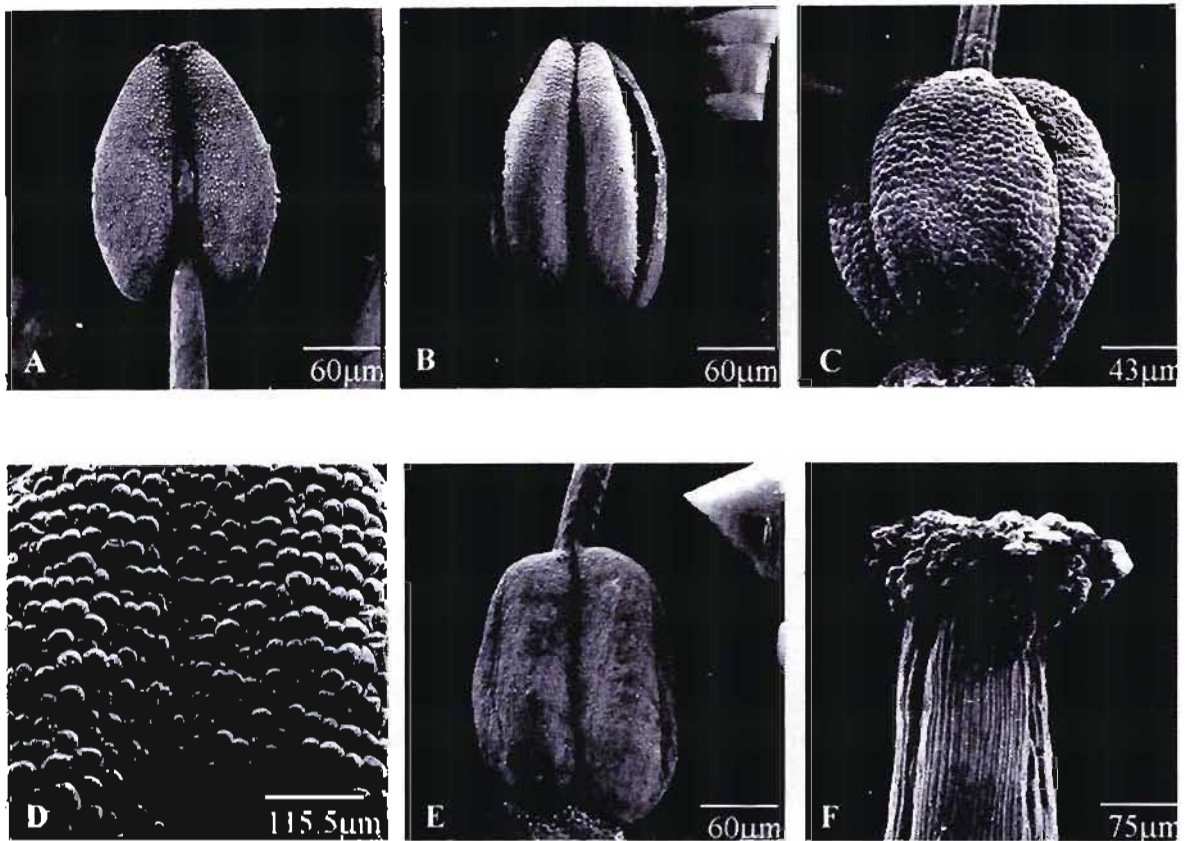


Figure 31. Scanning electron micrographs to illustrate A & B, anthers of *L. aloides* var. *bonaspei* (Duncan 125); C, obovoid ovary of *L. angelica* (Duncan 244); D, epidermal cells of ovary of *L. angelica* (Duncan 244); E, ellipsoid ovary of *L. arbuthnotiae* (Duncan 393); F, style and capitate stigma of *L. aloides* var. *bonaspei* (Duncan 125).

Six stamen characters were defined for the cladistic analyses:

1) **Filament orientation at anthesis.** Four states occurred: straight (=0); narrowly spreading (=1); recurved (=2) and declinate (=3). Quantitative character, scored as character 50 (Appendix 1).

In *Massonia* filaments were straight (radiating up to 10 degrees from the longitudinal axis). Within *Lachenalia* filament orientation was quite variable. Straight filaments occurred

in 67 (56%) ingroup species (63 *Lachenalia*, four *Polyxena*) (Figure 30A). In eight (7%) *Lachenalia* species filaments radiated 15-18 degrees from the longitudinal axis and were not recurved in the upper half (termed narrowly spreading in this text) (Figure 30B). In 11 (9%) *Lachenalia* and *Polyxena* species (10 *Lachenalia*, one *Polyxena*) filaments were recurved in the upper half and radiated 22-25 degrees from the longitudinal axis (Figure 30C). Filament orientation in 34 (28%) *Lachenalia* species was further modified to bent downwards 30-40 degrees from the longitudinal axis (termed declinate in this text) (Figures 30D, 32, Table 34).

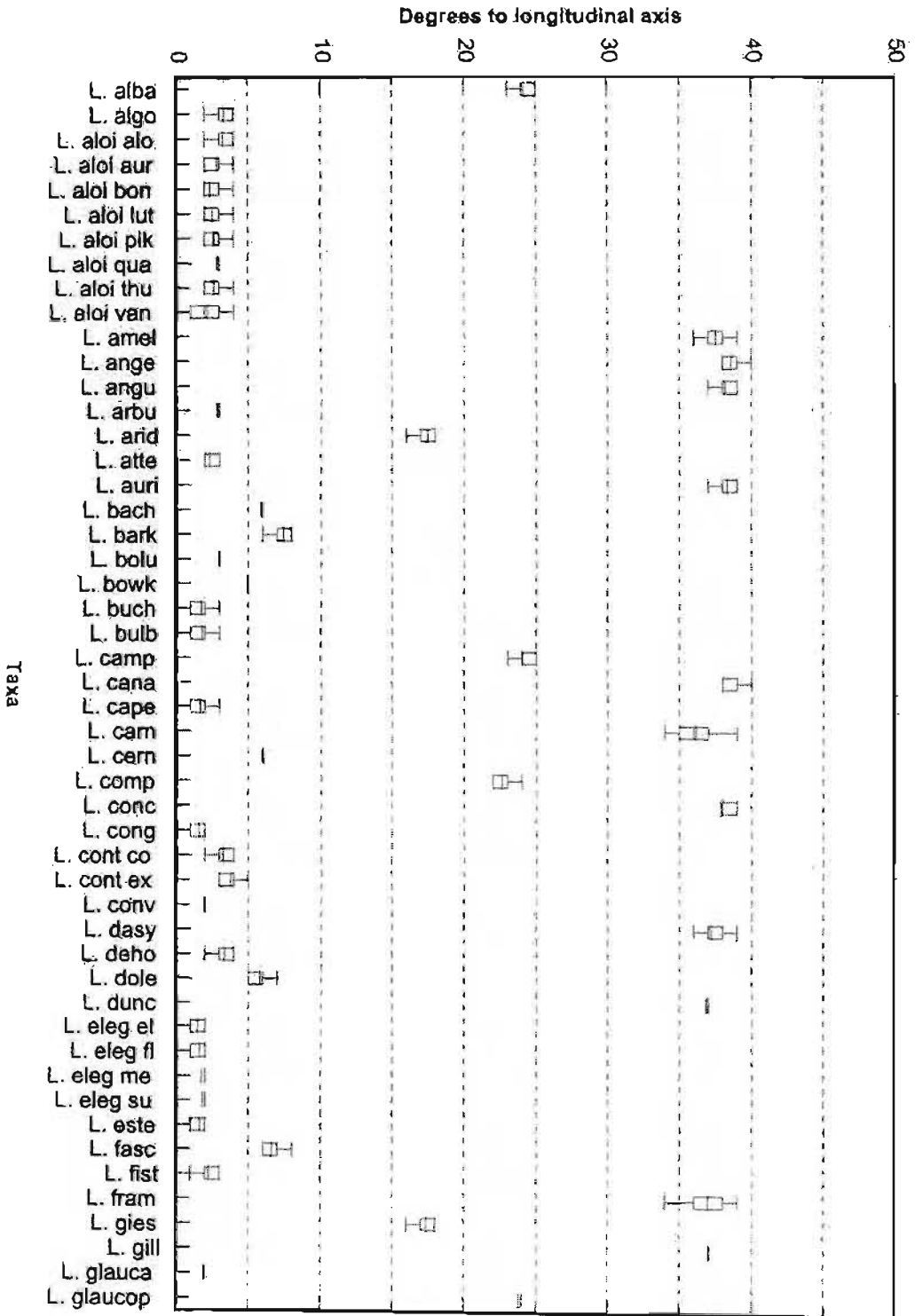


Figure 32. Filament orientation in Lachemalia and Polyxena

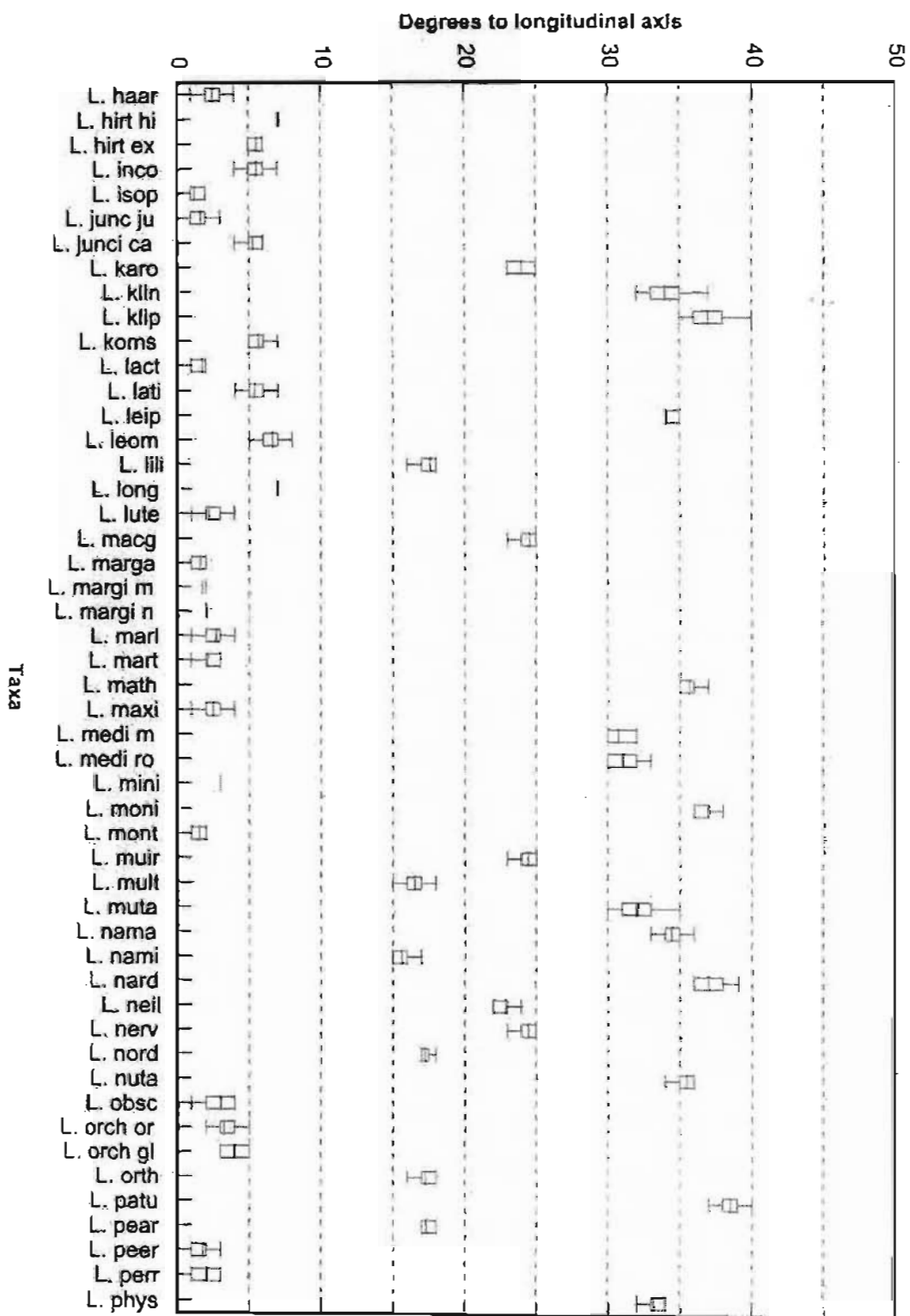


Figure 32. Filament orientation in Lachnella and Polyxena

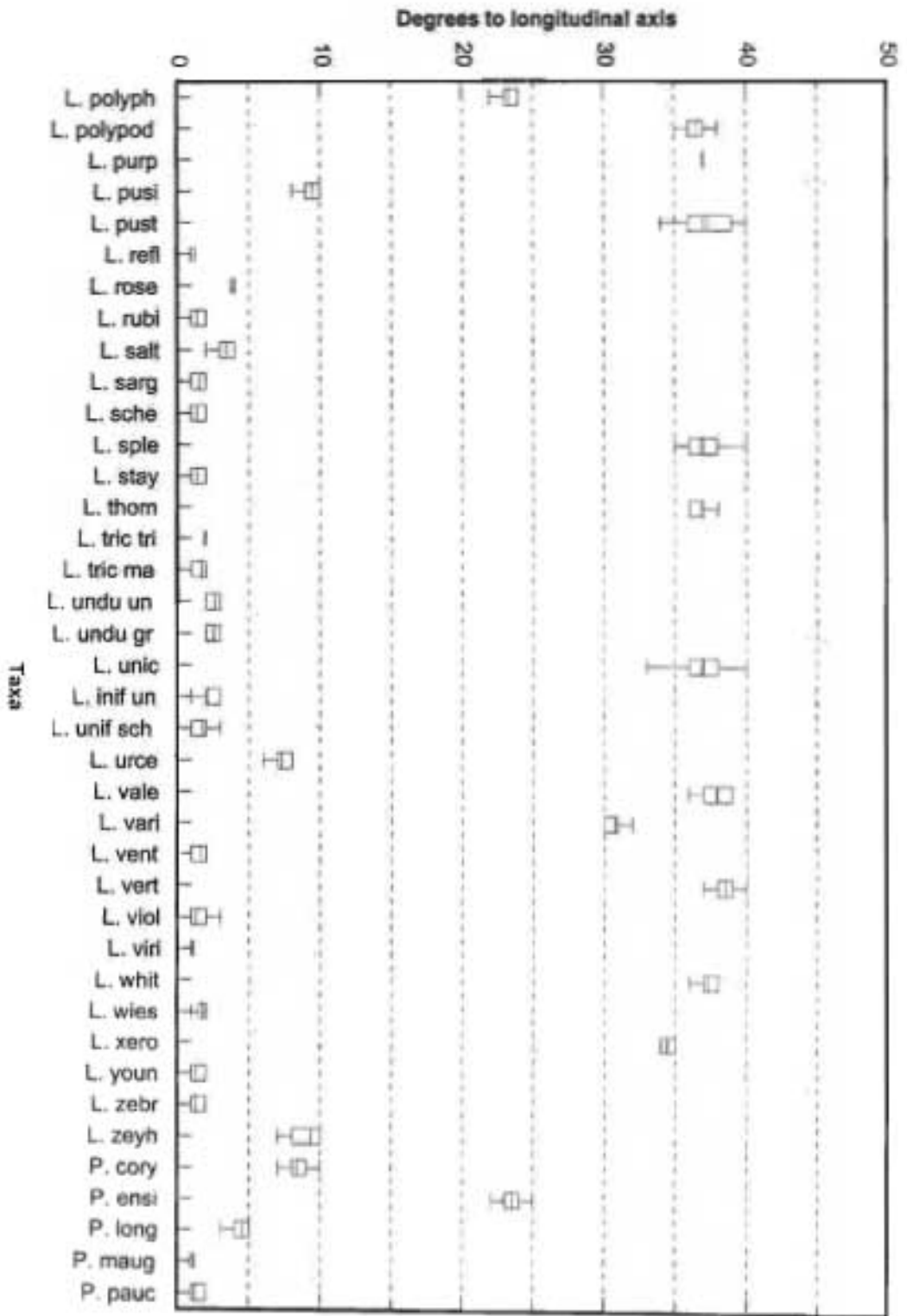


Figure 32. Filament orientation in Lichenalia and Polyxena

Table 34. Variation in filament orientation at anthesis in <i>Lachenalia</i> , <i>Polyxena</i> and the outgroup <i>Massonia</i>	
Character State	Species
Straight	<i>L. algoensis</i> , <i>L. aloides</i> (all eight varieties), <i>L. arbuthnotiae</i> , <i>L. attenuata</i> , <i>L. bachmannii</i> , <i>L. barkeriana</i> , <i>L. bolusii</i> , <i>L. bowkeri</i> , <i>L. buchbergensis</i> , <i>L. bulbifera</i> , <i>L. capensis</i> , <i>L. cernua</i> , <i>L. congesta</i> , <i>L. contaminata</i> (both varieties), <i>L. convallarioides</i> , <i>L. dehoopensis</i> , <i>L. doleritica</i> , <i>L. elegans</i> (all four varieties), <i>L. esterhuysenae</i> , <i>L. fasciculata</i> , <i>L. fistulosa</i> , <i>L. glauca</i> , <i>L. haarlemensis</i> , <i>L. hirta</i> (both varieties), <i>L. inconspicua</i> , <i>L. isopetala</i> , <i>L. juncifolia</i> (both varieties), <i>L. komsbergensis</i> , <i>L. lactosa</i> , <i>L. latimerae</i> , <i>L. leomontana</i> , <i>L. longibracteata</i> , <i>L. lutea</i> , <i>L. margaretae</i> , <i>L. marginata</i> (both subspecies), <i>L. marlothii</i> , <i>L. martinae</i> , <i>L. maximiliani</i> , <i>L. minima</i> , <i>L. montana</i> , <i>L. obscura</i> , <i>L. orchioides</i> (both varieties), <i>L. peersii</i> , <i>L. perryae</i> , <i>L. pusilla</i> , <i>L. reflexa</i> , <i>L. rosea</i> , <i>L. rubida</i> , <i>L. salteri</i> , <i>L. sargeantii</i> , <i>L. schelpei</i> , <i>L. stayneri</i> , <i>L. trichophylla</i> (both subspecies), <i>L. undulata</i> (both subspecies), <i>L. unifolia</i> (both varieties), <i>L. urceolata</i> , <i>L. ventricosa</i> , <i>L. violacea</i> , <i>L. viridiflora</i> , <i>L. wiesei</i> , <i>L. youngii</i> , <i>L. zebrina</i> , <i>L. zeyheri</i> <i>P. corymbosa</i> , <i>P. longituba</i> , <i>P. maughanii</i> , <i>P. paucifolia</i> <i>Massonia</i>
Narrowly spreading	<i>L. arida</i> , <i>L. giessii</i> , <i>L. liliiflora</i> , <i>L. multifolia</i> , <i>L. namibiensis</i> , <i>L. nordenstamii</i> , <i>L. orthopetala</i> , <i>L. pearsonii</i>
Recurved	<i>L. alba</i> , <i>L. campanulata</i> , <i>L. comptonii</i> , <i>L. glaucophylla</i> , <i>L. karooica</i> , <i>L. macgregoriorum</i> , <i>L. muirii</i> , <i>L. neilii</i> , <i>L. nervosa</i> , <i>L. polyphylla</i> <i>P. ensifolia</i>
Declinate	<i>L. ameliae</i> , <i>L. angelica</i> , <i>L. anguinea</i> , <i>L. aurioliae</i> , <i>L. canaliculata</i> , <i>L. carnosa</i> , <i>L. concordiana</i> , <i>L. dasybotrya</i> , <i>L. duncanii</i> , <i>L. framesii</i> , <i>L. gillettii</i> , <i>L. klinghardtiana</i> , <i>L. kliprandensis</i> , <i>L. leipoldtii</i> , <i>L. mathewsii</i> , <i>L. mediana</i> (both varieties), <i>L. moniliformis</i> , <i>L. mutabilis</i> , <i>L. namaquensis</i> , <i>L. nardouwensis</i> , <i>L. nutans</i> , <i>L. patula</i> , <i>L. physocaulos</i> , <i>L. polypodantha</i> , <i>L. purpureocaerulea</i> , <i>L. pustulata</i> , <i>L. splendida</i> , <i>L. thomasiae</i> , <i>L. unicolor</i> , <i>L. valeriae</i> , <i>L. variegata</i> , <i>L. verticillata</i> , <i>L. whitehillensis</i> , <i>L. xerophila</i>

2) **Filament colour.** Three states occurred: white for the entire length (=0); white in proximal portion, purple or magenta in distal portion (=1), and polymorphic (=2). Qualitative character, scored as character 51 (Appendix 1).

Massonia and 109 (91%) ingroup species (105 *Lachenalia*, four *Polyxena*) had white filaments. Ten (8%) *Lachenalia* species had filaments that were white in the lower half and purple or magenta in the upper half (*L. comptonii*, *L. duncanii*, *L. haarlemensis*, *L. macgregoriorum*, *L. nordenstamii*, *L. physocaulos*, *L. polypodantha*, *L. purpureocaerulea*, *L. splendida* and *L. violacea*), and in *P. ensifolia* filament colour was polymorphic.

3) **Filament length.** Two discontinuous states occurred: short filaments (=0); and long filaments (=1). Quantitative character, scored as character 52 (Appendix 1).

Filament length of *Massonia* and 132 (95%) ingroup taxa (127 *Lachenia*, all five *Polyxena*), was short, in which the filaments were up to 17 mm long (Figure 30B-D). Seven *Lachenia* taxa had long filaments, *L. aloides* var. *aloides*, *L. aloides* var. *aurea* (Figure 30A), *L. aloides* var. *bonaspei*, *L. aloides* var. *piketbergensis*, *L. aloides* var. *quadricolor*, *L. bulbifera* and *L. rubida*, in which the filaments were 20 mm long or longer (Figure 33, Table 35).

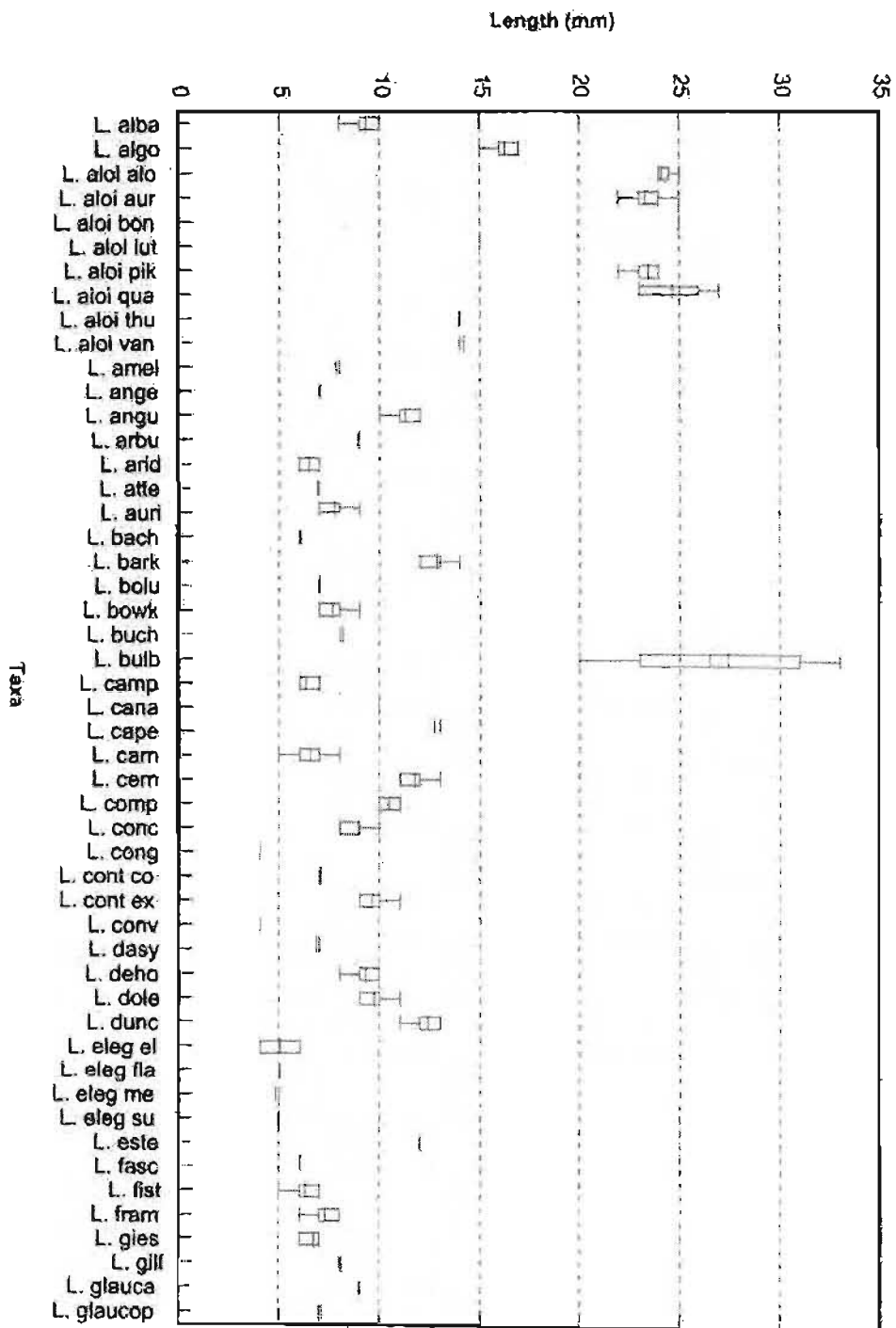


Figure 33. Filament length in *Lachenaelia* and *Polyxena*

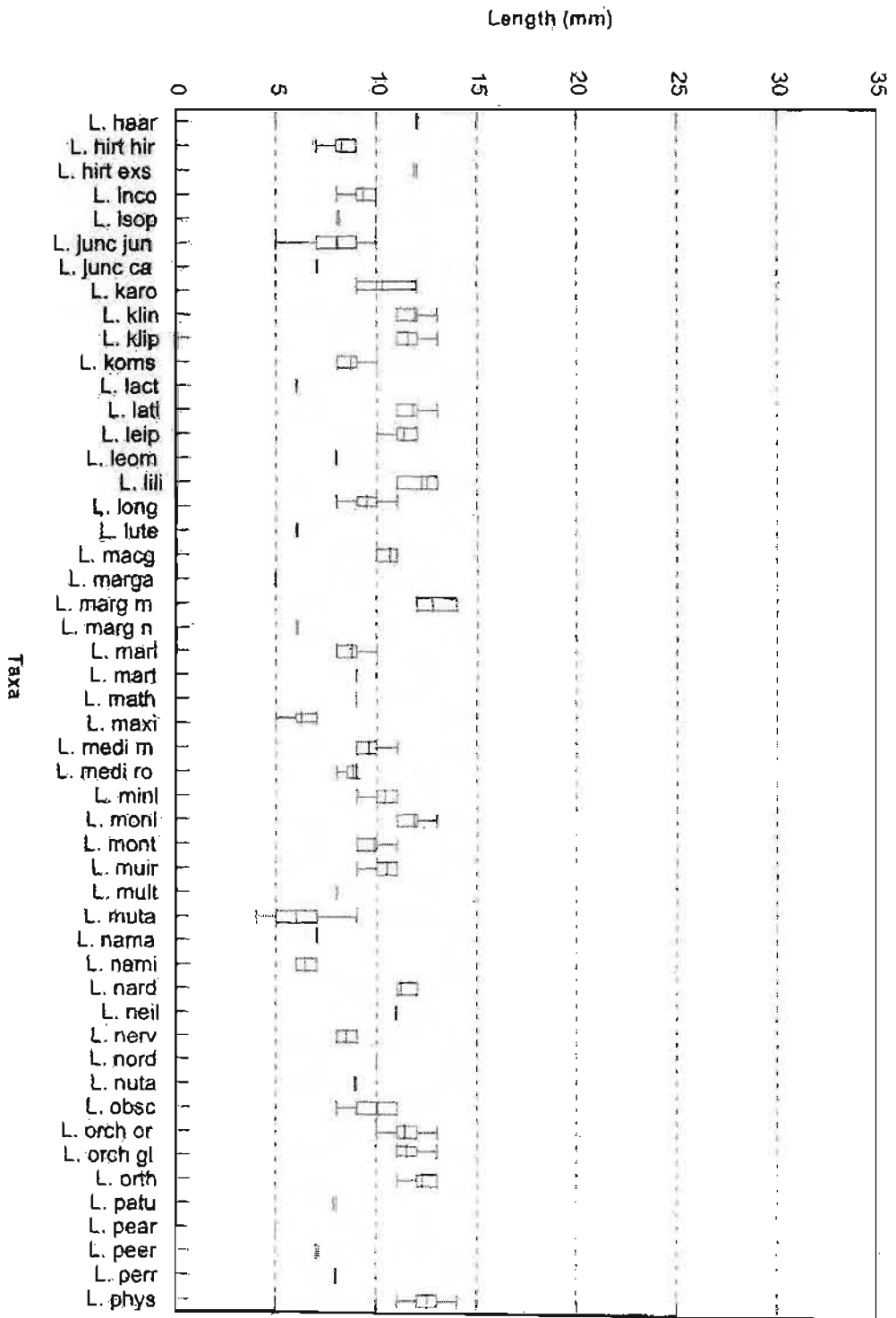


Figure 33. Filament length in Lachenalia and Polyxena

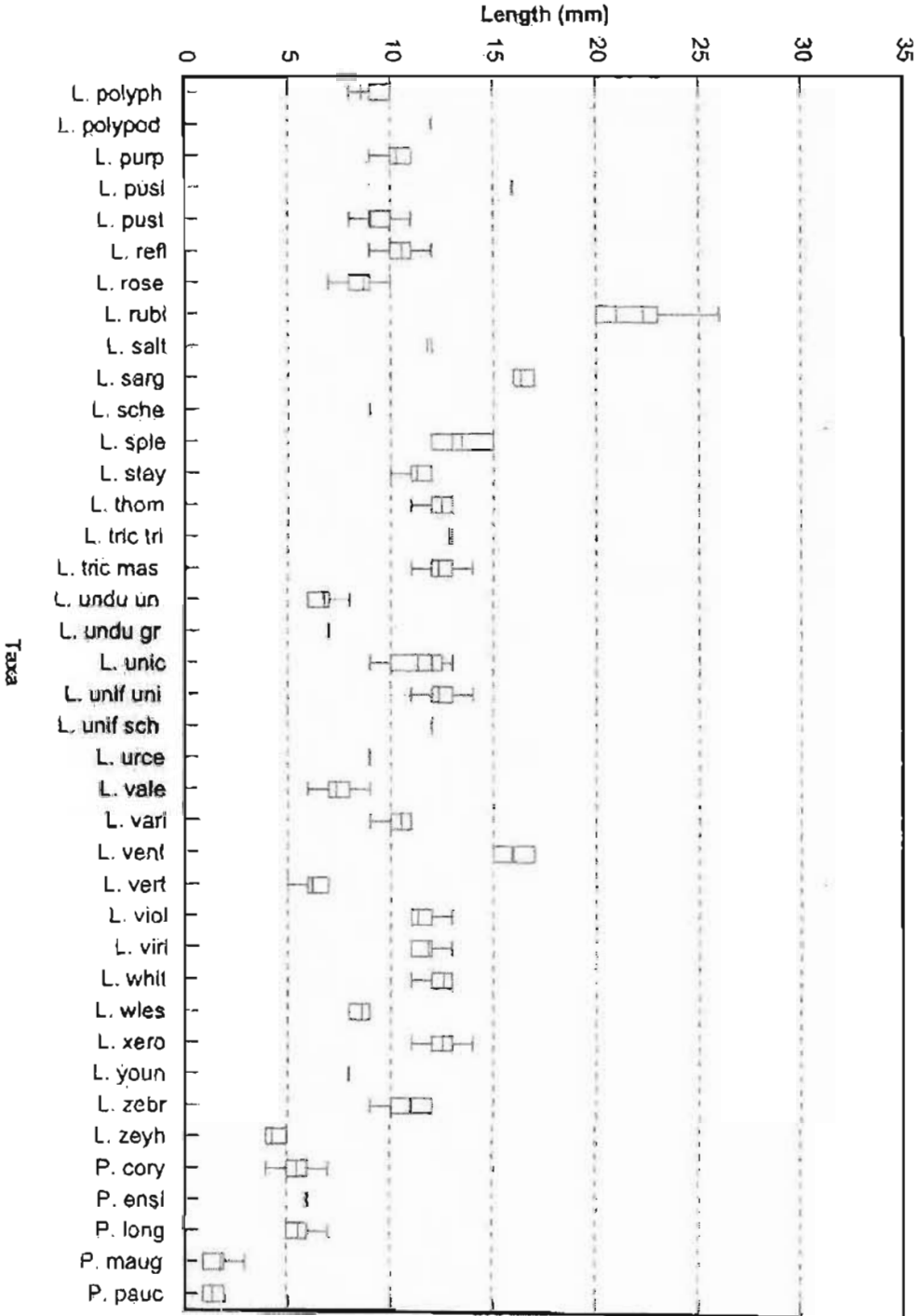


Figure 33. Filament length in Lachenalia and Polyxena

Table 35. Variation in filament length and insertion positions in *Lachenalia*, *Polyxena* and the outgroup *Massonia*

Species	Outer Filament Insertion	Outer Filament Length in mm	Inner Filament Insertion	Inner Filament Length in mm	Anthers
<i>L. alba</i>	medial	9-10	upper	8-9	included
<i>L. algoensis</i>	medial	16-17	upper	15-16	included
<i>L. aloides</i> var. <i>aloides</i>	basal	24-25	medial	23-24	included
<i>L. aloides</i> var. <i>aurea</i>	basal	23-25	medial	22-23	included
<i>L. aloides</i> var. <i>bonaspei</i>	basal	25-26	medial	24-25	included
<i>L. aloides</i> var. <i>luteola</i>	basal	15-16	medial	14-15	included
<i>L. aloides</i> var. <i>piketbergensis</i>	basal	23-24	medial	22-23	included
<i>L. aloides</i> var. <i>quadricolor</i>	basal	25-27	medial	23-25	included
<i>L. aloides</i> var. <i>thunbergii</i>	basal	14-15	medial	13-14	included
<i>L. aloides</i> var. <i>vanzyliae</i>	basal	14-16	medial	13-15	exserted
<i>L. ameliae</i>	medial	8-9	upper	7-8	included
<i>L. angelica</i>	medial	7-8	upper	6-7	exserted
<i>L. anguinea</i>	medial	11-12	upper	10-11	exserted
<i>L. arbutnotiae</i>	medial	9-10	upper	8-9	included
<i>L. arida</i>	medial	6-7	upper	6-7	exserted
<i>L. attenuata</i>	medial	7-8	upper	6-7	included
<i>L. aurioliae</i>	medial	7-9	upper	7-8	exserted
<i>L. bachmannii</i>	medial	5-7	upper	5-7	included
<i>L. barkeriana</i>	medial	12-14	upper	12-13	exserted
<i>L. bolusii</i>	medial	7-8	upper	6-7	included
<i>L. bowkeri</i>	medial	8-9	upper	7-8	included or exserted
<i>L. buchbergensis</i>	medial	9	upper	8	included
<i>L. bulbifera</i>	basal	21-33	medial	20-30	included
<i>L. campanulata</i>	medial	6-7	upper	6-7	exserted
<i>L. canaliculata</i>	medial	10-11	upper	9-10	included
<i>L. capensis</i>	medial	12-13	upper	11-12	included
<i>L. carnosa</i>	medial	6-9	upper	5-8	included
<i>L. cernua</i>	medial	12-13	upper	11-12	exserted
<i>L. comptonii</i>	medial	10-11	upper	10-11	exserted
<i>L. concordiana</i>	medial	9-10	upper	8-9	included
<i>L. congesta</i>	medial	4-5	upper	3-4	included
<i>L. contaminata</i> var. <i>contaminata</i>	medial	7-8	upper	6-7	included
<i>L. contaminata</i> var. <i>exserta</i>	medial	10-11	upper	9-10	exserted
<i>L. convallarioides</i>	medial	4	upper	4	included
<i>L. dasybotrya</i>	medial	7-8	upper	6-7	exserted
<i>L. dehoopensis</i>	medial	9-10	upper	8-9	included
<i>L. doleritica</i>	medial	10-11	upper	9-10	included
<i>L. duncanii</i>	medial	12-13	upper	11-12	exserted
<i>L. elegans</i> var. <i>elegans</i>	medial	5-6	upper	4-5	included
<i>L. elegans</i> var. <i>flava</i>	medial	5-6	upper	4-5	included
<i>L. elegans</i> var. <i>membranacea</i>	medial	5-6	upper	4-5	included
<i>L. elegans</i> var. <i>suaveolens</i>	medial	4-6	upper	4-5	included
<i>L. esterhuysenae</i>	medial	12-13	upper	11-12	exserted
<i>L. fasciculata</i>	medial	6-7	upper	5-6	included
<i>L. fistulosa</i>	medial	6-7	upper	5-6	included
<i>L. framesii</i>	medial	6-8	upper	6-7	included
<i>L. giesstii</i>	medial	6-7	upper	6-7	exserted
<i>L. gillettii</i>	medial	8-9	upper	7-8	exserted
<i>L. glauca</i>	medial	9-10	upper	8-9	exserted

Table 35. Variation in filament length and insertion positions in *Lachenalia*, *Polyxena* and the outgroup *Massonia*

Species	Outer Filament Insertion	Outer Filament Length in mm	Inner Filament Insertion	Inner Filament Length in mm	Anthers
<i>L. glaucophylla</i>	medial	7-8	upper	7-8	exserted
<i>L. haarlemensis</i>	medial	12-13	upper	11-12	exserted
<i>L. hirta</i> var. <i>hirta</i>	medial	7-9	upper	7-9	included
<i>L. hirta</i> var. <i>exserta</i>	medial	12-13	upper	11-12	exserted
<i>L. inconspicua</i>	medial	9-10	upper	8-9	included
<i>L. isopetala</i>	medial	8-9	upper	7-8	excluded
<i>L. juncifolia</i> var. <i>juncifolia</i>	medial	6-10	upper	5-9	exserted
<i>L. juncifolia</i> var. <i>campanulata</i>	medial	6-9	upper	6-8	exserted
<i>L. karooica</i>	medial	10-12	upper	9-11	exserted
<i>L. klinghardtiana</i>	medial	11-13	upper	11-12	exserted
<i>L. kliprandensis</i>	medial	12-13	upper	11-12	exserted
<i>L. komsbergensis</i>	medial	9-10	upper	8-9	exserted
<i>L. lactosa</i>	medial	6-7	upper	5-6	exserted
<i>L. latimerae</i>	medial	12-13	upper	11-12	exserted
<i>L. leipoldtii</i>	medial	11-12	upper	10-11	exserted
<i>L. leomontana</i>	medial	8-9	upper	7-8	included
<i>L. liliiflora</i>	medial	12-13	upper	11-12	included
<i>L. longibracteata</i>	medial	9-11	upper	8-10	exserted
<i>L. lutea</i>	medial	6-7	upper	5-6	included
<i>L. macgregoriorum</i>	medial	10-11	upper	10-11	exserted
<i>L. margaretae</i>	medial	5-6	upper	4-5	exserted
<i>L. marginata</i> subsp. <i>marginata</i>	medial	12-14	upper	12-13	included
<i>L. marginata</i> subsp. <i>neglecta</i>	medial	6-7	upper	5-6	included
<i>L. marlothii</i>	medial	9-10	upper	8-9	included
<i>L. martinae</i>	medial	9-10	upper	8-9	included
<i>L. mathewsii</i>	medial	9-10	upper	8-9	exserted
<i>L. maximiliani</i>	medial	6-7	upper	5-6	included
<i>L. mediana</i> var. <i>mediana</i>	medial	9-11	upper	9-10	included
<i>L. mediana</i> var. <i>rogersii</i>	medial	9-10	upper	8-9	included
<i>L. minima</i>	medial	10-11	upper	9-10	included
<i>L. moniliformis</i>	medial	12-13	upper	11-12	exserted
<i>L. montana</i>	medial	10-11	upper	9-10	exserted
<i>L. muirii</i>	medial	10-11	upper	9-10	included
<i>L. multifolia</i>	medial	8	upper	8	exserted
<i>L. mutabilis</i>	medial	4-9	upper	5-8	included
<i>L. namaquensis</i>	medial	7-8	upper	6-7	included
<i>L. namibiensis</i>	medial	6-7	upper	6-7	included
<i>L. nardouwensis</i>	medial	11-12	upper	9-10	exserted
<i>L. neilii</i>	medial	11-12	upper	10-11	exserted
<i>L. nervosa</i>	medial	8-9	upper	8-9	exserted
<i>L. nordenstamii</i>	medial	10	upper	10	exserted
<i>L. nutans</i>	medial	9-10	upper	8-9	exserted
<i>L. obscura</i>	medial	9-11	upper	8-10	included
<i>L. orchioides</i> var. <i>orchioides</i>	medial	11-14	upper	10-13	included
<i>L. orchioides</i> var. <i>glaucina</i>	medial	12-14	upper	11-13	included
<i>L. orthopetala</i>	medial	12-13	upper	11-12	included
<i>L. patula</i>	medial	8-9	upper	7-8	included
<i>L. pearsonii</i>	medial	5	upper	5	exserted
<i>L. peersii</i>	medial	7-8	upper	6-7	included
<i>L. perryae</i>	medial	8-9	upper	7-8	included

Table 35. Variation in filament length and insertion positions in *Lachenalia*, *Polyxena* and the outgroup *Massonia*

Species	Outer Filament Insertion	Outer Filament Length in mm	Inner Filament Insertion	Inner Filament Length in mm	Anthers
<i>L. physocaulos</i>	medial	12-14	upper	11-13	exserted
<i>L. polyphylla</i>	medial	9-10	upper	8-9	exserted
<i>L. polypodantha</i>	medial	12-13	upper	11-12	exserted
<i>L. purpureocaerulea</i>	medial	10-11	upper	9-10	exserted
<i>L. pusilla</i>	medial	16-17	upper	15-16	exserted
<i>L. pustulata</i>	medial	8-11	upper	7-9	exserted
<i>L. reflexa</i>	upper	11-12	upper	9-10	included
<i>L. rosea</i>	medial	8-10	upper	7-9	included
<i>L. rubida</i>	basal	21-26	medial	20-25	included
<i>L. salteri</i>	medial	12-13	upper	11-12	exserted
<i>L. sargeantii</i>	medial	17	upper	16	included
<i>L. schelpei</i>	medial	9-10	upper	8-9	exserted
<i>L. splendida</i>	medial	13-15	upper	11-13	exserted
<i>L. stayneri</i>	medial	11-12	upper	10-11	exserted
<i>L. thomasiae</i>	medial	12-13	upper	11-12	exserted
<i>L. trichophylla</i> subsp. <i>trichophylla</i>	medial	13-14	upper	12-13	included
<i>L. trichophylla</i> subsp. <i>massonii</i>	medial	11-14	upper	10-13	included
<i>L. undulata</i> subsp. <i>undulata</i>	medial	7-8	upper	6-7	included
<i>L. undulata</i> subsp. <i>grandifolia</i>	medial	7-8	upper	6-7	included
<i>L. unicolor</i>	medial	10-13	upper	9-12	exserted
<i>L. unifolia</i> var. <i>unifolia</i>	medial	10-14	upper	9-13	included
<i>L. unifolia</i> var. <i>schlechteri</i>	medial	12-13	upper	11-12	included
<i>L. urceolata</i>	medial	9-10	upper	8-9	included
<i>L. valeriae</i>	medial	7-9	upper	6-8	included
<i>L. variegata</i>	medial	10-11	upper	9-10	exserted
<i>L. ventricosa</i>	medial	16-17	upper	15-16	exserted
<i>L. verticillata</i>	medial	6-7	upper	5-6	included
<i>L. violacea</i>	medial	10-13	upper	9-11	exserted
<i>L. viridiflora</i>	upper	12-13	upper	11-12	included
<i>L. whitehillensis</i>	medial	12-13	upper	11-12	exserted
<i>L. wiesei</i>	medial	9	upper	8	included
<i>L. xerophila</i>	medial	12-14	upper	11-12	exserted
<i>L. youngii</i>	medial	8-9	upper	7-8	exserted
<i>L. zebrina</i>	medial	10-12	upper	9-11	exserted
<i>L. zeyheri</i>	medial	4-5	upper	4-5	included
<i>P. corymbosa</i>	medial	5-7	upper	4-6	exserted
<i>P. ensifolia</i>	upper	5-7	upper	4-7	exserted
<i>P. longituba</i>	upper	5-7	upper	4-5	included
<i>P. maughanii</i>	upper	2-3	upper	1-2	included
<i>P. paucifolia</i>	upper	1-2	upper	1	included
<i>Massonia</i>	upper	7-17	upper	7-17	exserted

4) **Filament relative lengths.** Two states occurred: inner and outer filaments equal (=0); and inner and outer filaments subequal (=1). Qualitative character, scored as character 53 (Appendix 1).

Equal inner and outer filaments occurred in *Massonia*. Similarly, 14 (12%) *Lachenalia* species with narrowly campanulate or widely campanulate flowers, *L. arida*, *L. bachmannii*, *L. campanulata*, *L. comptonii* (Figure 25D), *L. convallarioides*, *L. giessii*, *L. glaucophylla*, *L. macgregorium*, *L. multifolia*, *L. namibiensis*, *L. nervosa*, *L. nordenstamii*, *L. pearsonii* and *L. zeyheri*, had equal filaments. In 106 (88%) *Lachenalia* and *Polyxena* species (101 *Lachenalia*, all five *Polyxena*), filament length was subequal (Table 35).

5) **Outer filament insertion.** Three states occurred: upper (=0); medial (=1); and basal (=2). Qualitative character, scored as character 54 (Appendix 1).

In *Massonia* the outer filaments were inserted at the mouth of the perianth tube. This arrangement also occurred in six (5%) ingroup species, *L. reflexa*, *L. viridiflora*, *P. ensifolia*, *P. longituba*, *P. maughanii* and *P. paucifolia*. In three (2.5%) *Lachenalia* species the outer filaments were inserted at the base of the perianth tube, *L. aloides* (all eight varieties), *L. bulbifera* and *L. rubida*. Most of the species had the outer filaments inserted in the middle of the perianth tube, 111 (92.5%) ingroup species (110 *Lachenalia* species and *P. corymbosa*) (Table 35).

6) **Inner filament insertion.** Two states occurred: upper (=0); and medial (=1). Qualitative character, scored as character 55 (Appendix 1).

The inner filaments of *Massonia* and 117 (97.5%) ingroup species (112 *Lachenalia*, all five *Polyxena*) were inserted in the perianth mouth. In three (2.5%) *Lachenalia* species the inner filaments were inserted in the middle of the perianth tube, *L. aloides* (all eight varieties), *L. bulbifera* and *L. rubida* (Table 35).

5.16 POLLEN

Monocotyledon pollen morphology is conservative and is relatively poorly represented in fossil records (Harley & Zavada 2000). The polar and equatorial regions of monocotyledonous pollen are often difficult to define concisely, and they have a tendency toward thin exines. Sulcate pollen dominates in the Liliiflorae (Dahlgren & Clifford 1982). Uniaperturate, sulcate pollen with a longitudinal groove along the distal face is considered a conservative feature and is widespread in monocotyledons, as opposed to the multi-aperturate pollen characteristic of the dicotyledons (Cronquist 1988).

5.16.1 Materials and Methods

Electron microscopy

Pollen samples were collected and placed in vials containing 70% ethanol. Anthers containing ripe pollen were mounted onto stubs with double-sided tape, allowed to dry overnight, then sputter-coated with gold-palladium and viewed with an Hitachi S-570 scanning electron microscope at an acceleration voltage of 10 kV.

5.16.2 Results

Pollen in *Lachenalia* and *Polyxena* was consistently monosulcate. Pollen grains were isopolar, and the surface topography of the exine was of some diagnostic value in that it was reticulate in the majority of species (Erdtman 1969), or rugose. The sulcus was located at the distal pole of the pollen grain and the proximal pole had a prominent median ridge. Dehydration of the pollen grain caused the sulcus to close. There was slight variation in the shape, degree of reticulation and size of pollen grains, which varied from 21-30 x 12-15 μm . These characters were however geographically unstable and were not used in the cladistic analyses.

One pollen character was defined for the cladistic analyses:

1) **Exine sculpturing.** Two states occurred: rugose (=0); and reticulate (=1). Qualitative character, scored as character 56 (Appendix 1).

Massonia had a rugose exine. Out of the 116 ingroup species investigated, 19 (16%) species had a rugose pollen exine (14 *Lachenalia*, all five *Polyxena*) (Figure 34A-G). In 97 (84%) *Lachenalia* species, the pollen exine was reticulate (Figure 34H-L, Table 36).

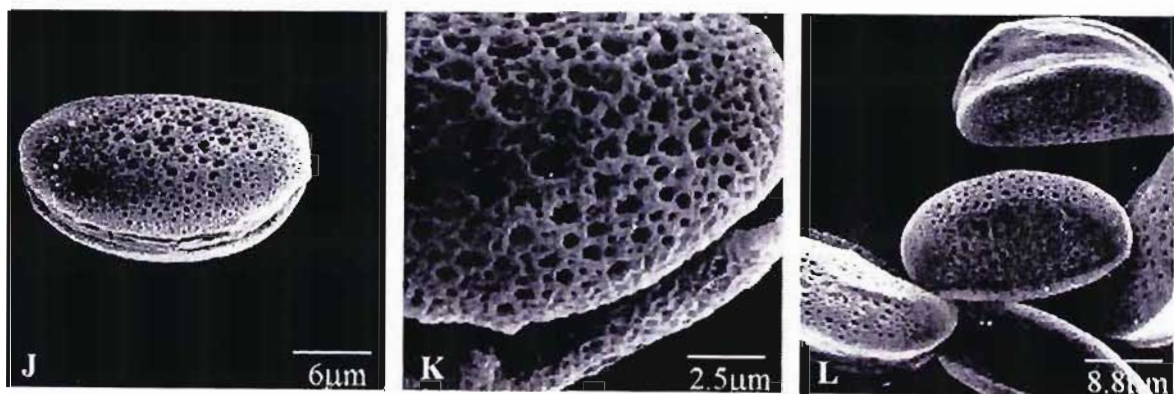
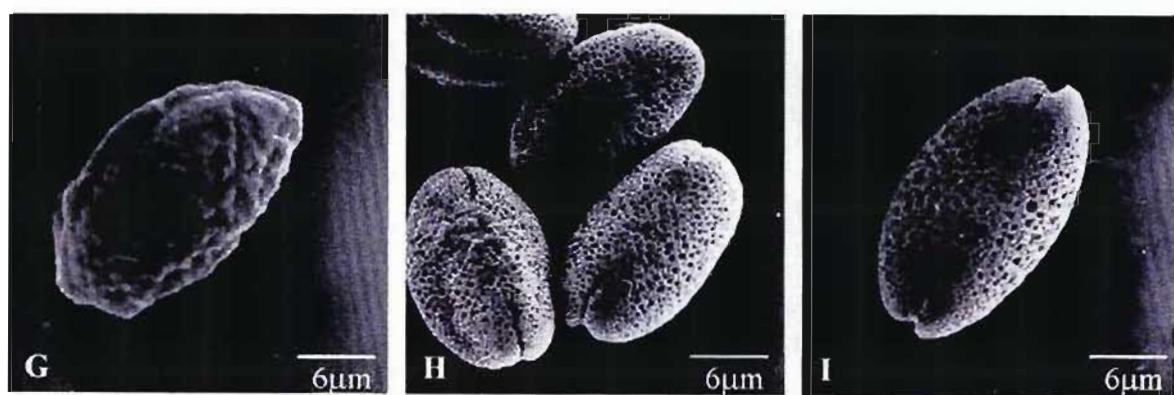
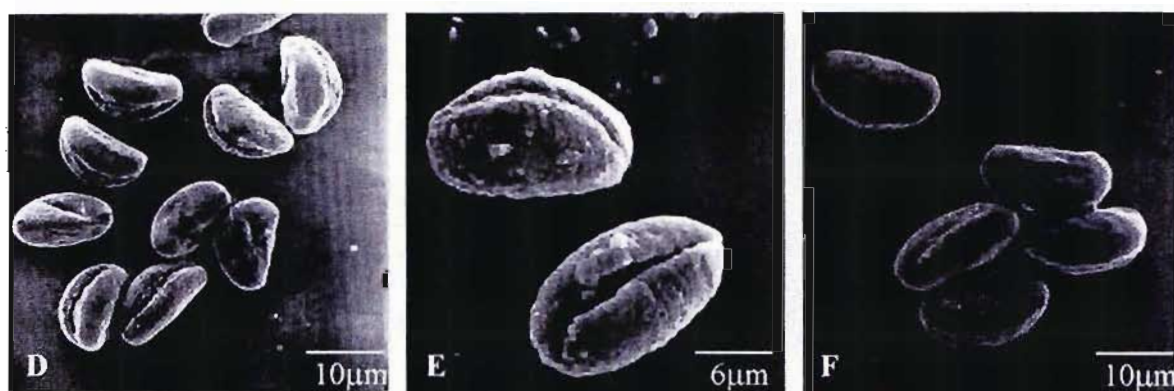
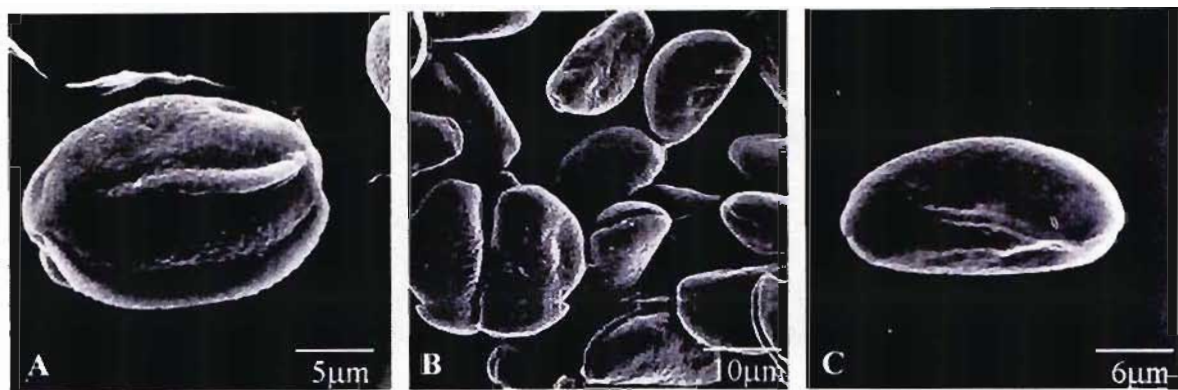


Table 36. Variation in pollen exine sculpturing in *Lachenalia*, *Polyxena* and the outgroup *Massonia*

Character State	Species
Rugose	<i>L. angelica</i> , <i>L. isopetala</i> , <i>L. juncifolia</i> (both varieties), <i>L. komsbergensis</i> , <i>L. macgregoriorum</i> , <i>L. multifolia</i> , <i>L. namibiensis</i> , <i>L. patula</i> , <i>L. peersii</i> , <i>L. polyphylla</i> , <i>L. rosea</i> , <i>L. salteri</i> , <i>L. trichophylla</i> (both subspecies), <i>L. unifolia</i> (both varieties) <i>P. corymbosa</i> , <i>P. ensifolia</i> , <i>P. longituba</i> , <i>P. maughanii</i> , <i>P. paucifolia</i> <i>Massonia</i>
Reticulate	<i>L. alba</i> , <i>L. algoensis</i> , <i>L. aloides</i> (all eight varieties), <i>L. ameliae</i> , <i>L. anguinea</i> , <i>L. arbutnotiae</i> , <i>L. arida</i> , <i>L. attenuata</i> , <i>L. aurioliae</i> , <i>L. bachmannii</i> , <i>L. barkeriana</i> , <i>L. bolusii</i> , <i>L. bowkeri</i> , <i>L. buchbergensis</i> , <i>L. bulbifera</i> , <i>L. campanulata</i> , <i>L. canaliculata</i> , <i>L. capensis</i> , <i>L. carnosa</i> , <i>L. cernua</i> , <i>L. comptonii</i> , <i>L. concordiana</i> , <i>L. congesta</i> , <i>L. contaminata</i> (both varieties), <i>L. convallarioides</i> , <i>L. dasybotrya</i> , <i>L. dehoopensis</i> , <i>L. doleritica</i> , <i>L. duncanii</i> , <i>L. elegans</i> (all four varieties), <i>L. fasciculata</i> , <i>L. fistulosa</i> , <i>L. framesii</i> , <i>L. giessii</i> , <i>L. gillettii</i> , <i>L. glauca</i> , <i>L. glaucophylla</i> , <i>L. haarlemensis</i> , <i>L. hirta</i> (both varieties), <i>L. inconspicua</i> , <i>L. karooica</i> , <i>L. klinghardtiana</i> , <i>L. kliprandensis</i> , <i>L. lactosa</i> , <i>L. latimerae</i> , <i>L. leipoldtii</i> , <i>L. leomontana</i> , <i>L. liliiflora</i> , <i>L. longibracteata</i> , <i>L. lutea</i> , <i>L. margaretae</i> , <i>L. marginata</i> (both subspecies), <i>L. marlothii</i> , <i>L. martinae</i> , <i>L. mathewsii</i> , <i>L. maximiliani</i> , <i>L. mediana</i> (both varieties), <i>L. minima</i> , <i>L. moniliformis</i> , <i>L. montana</i> , <i>L. muiirii</i> , <i>L. mutabilis</i> , <i>L. namaquensis</i> , <i>L. nardouwensis</i> , <i>L. neilii</i> , <i>L. nervosa</i> , <i>L. obscura</i> , <i>L. orchioides</i> (both varieties), <i>L. orthopetala</i> , <i>L. pearsonii</i> , <i>L. perryae</i> , <i>L. physocaulos</i> , <i>L. polypodantha</i> , <i>L. purpureocaerulea</i> , <i>L. pusilla</i> , <i>L. pustulata</i> , <i>L. reflexa</i> , <i>L. rubida</i> , <i>L. schelppei</i> , <i>L. splendida</i> , <i>L. stayneri</i> , <i>L. thomasiae</i> , <i>L. undulata</i> (both subspecies), <i>L. unicolor</i> , <i>L. urceolata</i> , <i>L. valeriae</i> , <i>L. variegata</i> , <i>L. ventricosa</i> , <i>L. verticillata</i> , <i>L. violacea</i> , <i>L. viridiflora</i> , <i>L. whitehillensis</i> , <i>L. wiesei</i> , <i>L. youngii</i> , <i>L. zebrina</i> , <i>L. zeyheri</i>

5.17 GYNOECIUM

5.17.1 Materials and methods

Determination of stigma receptivity

Following Heslop-Harrison & Shirvanna's (1977) methodology, stigmas at different stages of development were sampled from a selection of *Lachenalia* and *Polyxena* species with different flower shapes and tested to determine at which stage they became receptive, for possible use as a character in the cladistic analyses. Stigmas were placed in a droplet of 3% hydrogen peroxide on a microscope slide, mounted with a cover slip and viewed under a light microscope.

15.17.2 Results

No reaction was observed from stigmas sampled from flowers at anthesis or day one. Stigmas sampled from flowers that were two and three days old indicated partial receptivity and bubbled slowly. The stigmas of four-day-old flowers with fully ripe anthers were receptive and bubbled strongly. No maturation differences were observed in stigma receptivity across taxa with different flower shapes.

The gynoecium in *Lachenalia* and *Polyxena* had a simple, slender style with a capitate stigma, and an obovoid or ellipsoid ovary. Styles were terete and consisted of three stylar channels.

Ovaries in *Polyxena* and most *Lachenalia* species were sessile except for two taxa (*L. bolusii*, *L. elegans* var. *flava*) that were found to be shortly stipitate.

5.17.2.1 Style and Stigma

Style orientation at anthesis was either straight (radiating up to 10 degrees from the axis), or declinate. Styles were straight in species with straight, narrowly spreading and recurved filaments. The styles of species with declinate filaments were also declinate.

Styles were white in most species, but in all species in which the distal portion of the filaments was purple or magenta, the distal portion of the style or the style apex was also purple or magenta.

Styles were shortest in *P. paucifolia* (1-2 mm), *L. elegans* var. *flava* (2 mm) and *L. congesta* (2-3 mm). The longest styles occurred in (*L. bulbifera* (22-27 mm) and *L. rubida* (25-30 mm). For most species, style length fell between 7-12 mm. During fruiting, the styles of many species protruded conspicuously beyond the stamens and tip of the perianth as the

ovary enlarged. Style length was not used in the cladistic analyses as no discontinuous classes could be defined.

Stigmas were capitate in all species (Figure 31 F), and were positioned lower than, at the same level as, or higher than the anthers, such as in *L. congesta*, *L. margaretae* and *L. klinghardtiana*, respectively.

One style character was defined for the cladistic analyses :

1) **Style orientation at anthesis.** Two discontinuous states occurred: straight styles (=0); and declinate styles (=1). Quantitative character, scored as character 57 (Appendix 1).

Styles of *Massonia* were straight. Straight styles also occurred in 86 (72%) ingroup species (81 *Lachenalia*, all five *Polyxena*) in which the styles radiated up to 10 degrees from the longitudinal axis (Figure 30A-C). In 34 (28%) *Lachenalia* species style orientation was declinate (30-40 degrees from the longitudinal axis) (Figures 30D, 35, Table 37).

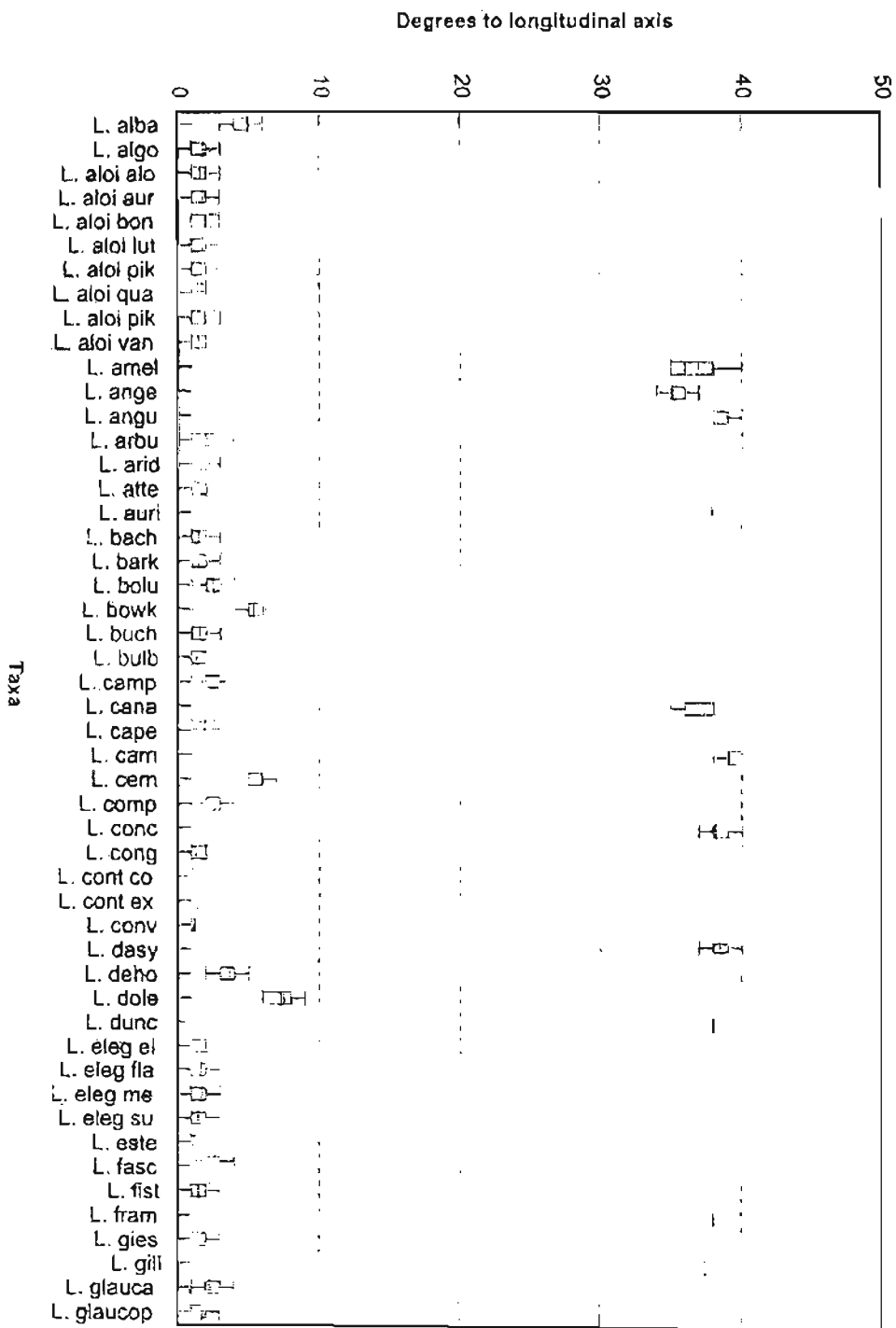


Figure 35. Style orientation in Lachenaelia and Polyxena

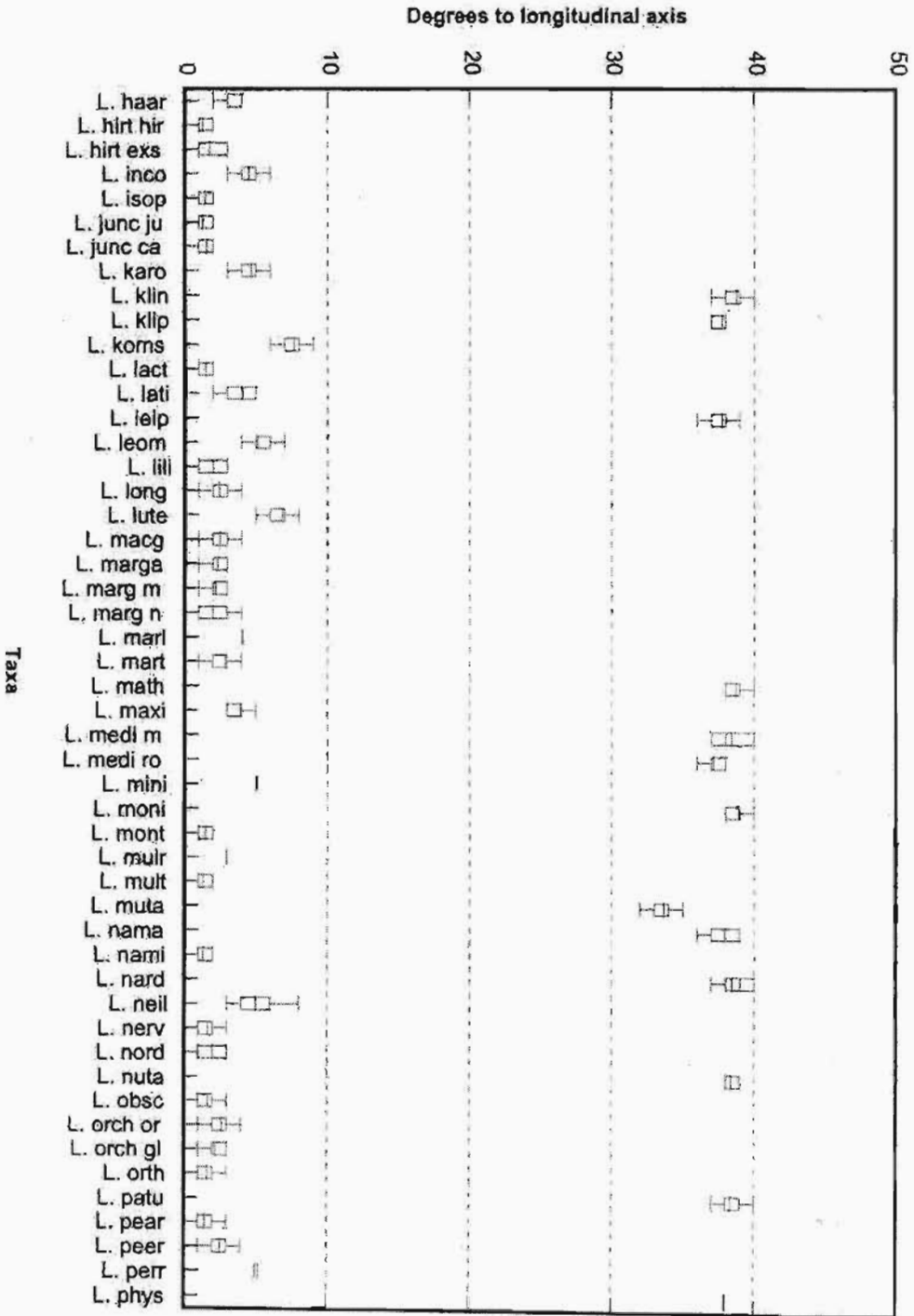


Figure 35. Style orientation in Lachenalia and Polyxena

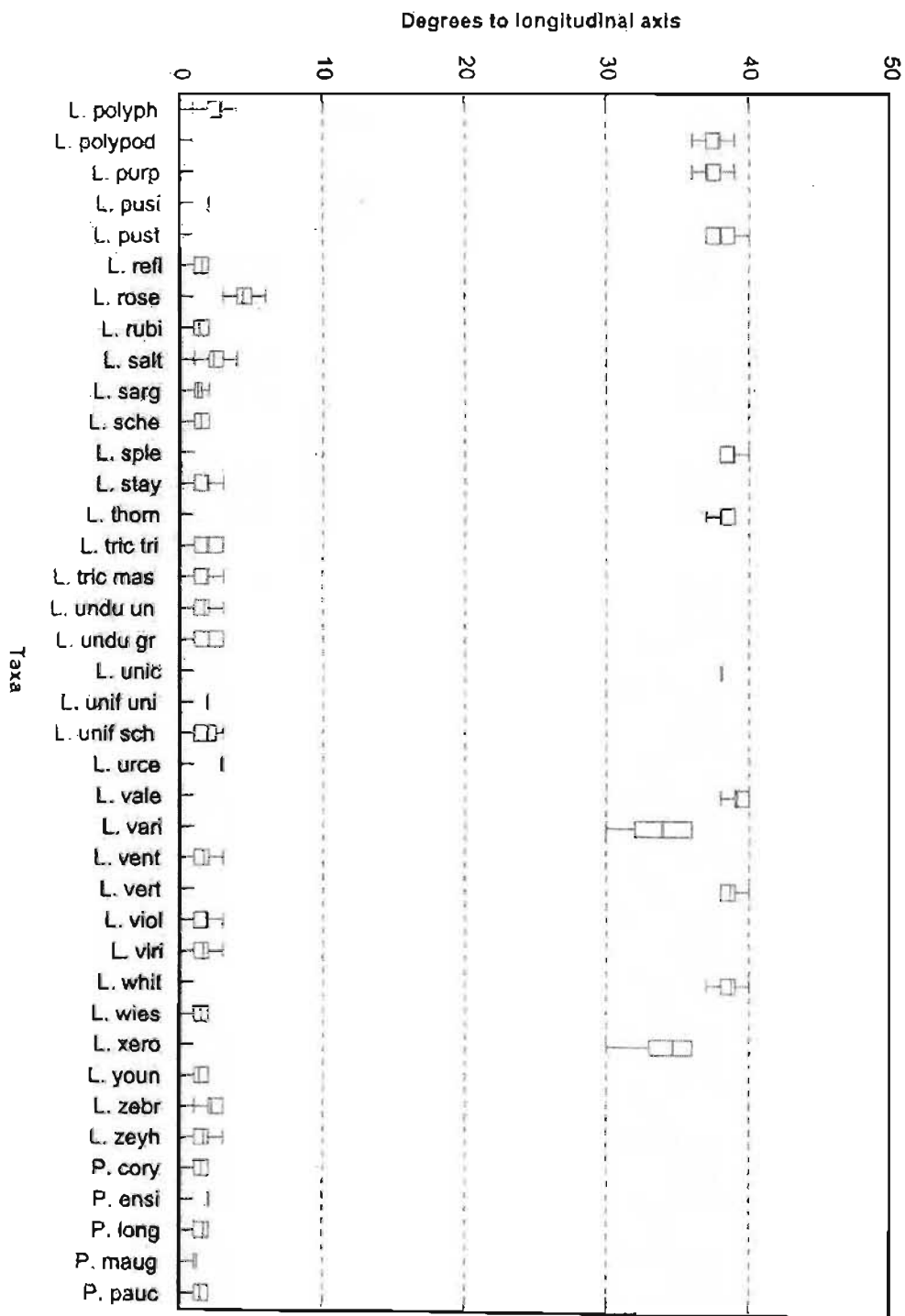


Figure 35. Style orientation in Lachenalia and Polyxena

Table 37. Variation in style orientation at anthesis in *Lachenalia*, *Polyxena* and the outgroup *Massonia*

Character State	Species
Straight	<p><i>L. alba</i>, <i>L. algoensis</i>, <i>L. aloides</i> (all eight varieties), <i>L. arbutnotiae</i>, <i>L. arida</i>, <i>L. attenuata</i>, <i>L. bachmannii</i>, <i>L. barkeriana</i>, <i>L. bolusii</i>, <i>L. bowkeri</i>, <i>L. buchbergensis</i>, <i>L. bulbifera</i>, <i>L. campanulata</i>, <i>L. capensis</i>, <i>L. cernua</i>, <i>L. comptonii</i>, <i>L. congesta</i>, <i>L. contaminata</i> (both varieties), <i>L. convallarioides</i>, <i>L. dehoopensis</i>, <i>L. doleritica</i>, <i>L. elegans</i> (all four varieties), <i>L. esterhuysenae</i>, <i>L. fasciculata</i>, <i>L. fistulosa</i>, <i>L. giessii</i>, <i>L. glauca</i>, <i>L. glaucophylla</i>, <i>L. haarlemensis</i>, <i>L. hirta</i> (both varieties), <i>L. inconspicua</i>, <i>L. isopetala</i>, <i>L. juncifolia</i> (both varieties), <i>L. karooica</i>, <i>L. komsbergensis</i>, <i>L. lactosa</i>, <i>L. latimerae</i>, <i>L. leomontana</i>, <i>L. liliiflora</i>, <i>L. longibracteata</i>, <i>L. lutea</i>, <i>L. macgregoriorum</i>, <i>L. margaretae</i>, <i>L. marginata</i> (both subspecies), <i>L. marlothii</i>, <i>L. martinae</i>, <i>L. maximiliani</i>, <i>L. minima</i>, <i>L. montana</i>, <i>L. muirii</i>, <i>L. multifolia</i>, <i>L. namibiensis</i>, <i>L. neilii</i>, <i>L. nervosa</i>, <i>L. nordenstamii</i>, <i>L. obscura</i>, <i>L. orchiioides</i> (both varieties), <i>L. orthopetala</i>, <i>L. pearsonii</i>, <i>L. peersii</i>, <i>L. perryae</i>, <i>L. polyphylla</i>, <i>L. pusilla</i>, <i>L. reflexa</i>, <i>L. rosea</i>, <i>L. rubida</i>, <i>L. salteri</i>, <i>L. sargeantii</i>, <i>L. schelpei</i>, <i>L. stayneri</i>, <i>L. trichophylla</i> (both subspecies), <i>L. undulata</i> (both subspecies), <i>L. unifolia</i> (both varieties), <i>L. urceolata</i>, <i>L. ventricosa</i>, <i>L. violacea</i>, <i>L. viridiflora</i>, <i>L. wiesei</i>, <i>L. youngii</i>, <i>L. zebrina</i>, <i>L. zeyheri</i> <i>P. corymbosa</i>, <i>P. ensifolia</i>, <i>P. longituba</i>, <i>P. maughanii</i>, <i>P. paucifolia</i> <i>Massonia</i></p>
Declinate	<p><i>L. ameliae</i>, <i>L. angelica</i>, <i>L. anguinea</i>, <i>L. aurioliae</i>, <i>canaliculata</i>, <i>L. carnosa</i>, <i>L. concordiana</i>, <i>L. dasybotrya</i>, <i>L. duncanii</i>, <i>L. framesii</i>, <i>L. gillettii</i>, <i>L. klinghardiana</i>, <i>L. kliprandensis</i>, <i>L. leipoldtii</i>, <i>mathewsii</i>, <i>L. mediana</i> (both varieties), <i>L. moniliformis</i>, <i>L. mutabilis</i>, <i>L. namaquensis</i>, <i>L. nardouwensis</i>, <i>L. nutans</i>, <i>L. patula</i>, <i>L. physocaulos</i>, <i>L. polypodantha</i>, <i>L. purpureocaerulea</i>, <i>L. pustulata</i>, <i>L. splendida</i>, <i>L. thomasiae</i>, <i>L. unicolor</i>, <i>L. valeriae</i>, <i>L. variegata</i>, <i>L. verticillata</i>, <i>L. whitehillensis</i>, <i>L. xerophila</i></p>

5.17.2.2 Ovary

The tricarpellary ovary was always syncarpic with axile placentation. Simple septal nectaries occurred in all *Lachenalia* and *Polyxena* species investigated, but nectar quantities varied greatly between different flower shapes. Species with long tubular flowers which are bird-pollinated such as *L. bulbifera* and *L. rubida*, contained much greater quantities of nectar than mellitophilous species with oblong-campanulate, narrowly campanulate, widely campanulate or urceolate flowers. Transverse sections through the ovaries revealed that the nectaries were located in the upper half of the ovary dome.

Ovules were produced in two rows and production per ovule was highly variable, ranging

from four (*L. congesta*) to twenty-six (*L. angelica*). Ovule number in most species ranged from 10-15 ovules per locule, but this varied with season and could not be used in the cladistic analyses.

One ovary character was defined for the cladistic analyses:

1) **Ovary shape.** Two states occurred: obovoid (=0); and ellipsoid (=1). Qualitative character, scored as character 58 (Appendix 1).

Ovaries of *Massonia* and 44 (32%) ingroup taxa (42 *Lachenalia*, two *Polyxena*) were obovoid (Figure 31C). In 95 (68%) taxa (92 *Lachenalia*, three *Polyxena*), ovaries were ellipsoid (Figure 31E, Table 38).

Table 38. Variation in ovary shape in <i>Lachenalia</i>, <i>Polyxena</i> and the outgroup <i>Massonia</i>	
Character State	Taxa
Obovoid	<i>L. angelica</i> , <i>L. anguinea</i> , <i>L. arida</i> , <i>L. attenuata</i> , <i>L. bolusii</i> , <i>L. campanulata</i> , <i>L. convallarioides</i> , <i>L. doleritica</i> , <i>L. duncanii</i> , <i>L. elegans</i> var. <i>elegans</i> , <i>L. esterhuysenae</i> , <i>L. giessii</i> , <i>L. glaucophylla</i> , <i>L. haarlemensis</i> , <i>L. hirta</i> (both varieties), <i>L. juncifolia</i> (both varieties), <i>L. komsbergensis</i> , <i>L. latimerae</i> , <i>L. leomontana</i> , <i>L. macgregoriorum</i> , <i>L. margaretae</i> , <i>L. moniliformis</i> , <i>L. montana</i> , <i>L. muirii</i> , <i>L. multifolia</i> , <i>L. namibiensis</i> , <i>L. nervosa</i> , <i>L. mutans</i> , <i>L. pearsonii</i> , <i>L. peersii</i> , <i>L. perryae</i> , <i>L. polyphylla</i> , <i>L. polypodantha</i> , <i>L. rosea</i> , <i>L. sargeantii</i> , <i>L. stayneri</i> , <i>L. whitehillensis</i> , <i>L. xerophila</i> , <i>L. youngii</i> , <i>L. zeyheri</i> <i>P. corymbosa</i> , <i>P. paucifolia</i> <i>Massonia</i>
Ellipsoid	<i>L. alba</i> , <i>L. algoensis</i> , <i>L. aloides</i> (all eight varieties), <i>L. ameliae</i> , <i>L. arbutnotiae</i> , <i>L. aurioliae</i> , <i>L. bachmannii</i> , <i>L. barkeriana</i> , <i>L. bowkeri</i> , <i>L. buchbergensis</i> , <i>L. bulbifera</i> , <i>L. canaliculata</i> , <i>L. capensis</i> , <i>L. carnosae</i> , <i>L. cernuae</i> , <i>L. comptonii</i> , <i>L. concordiana</i> , <i>L. congesta</i> , <i>L. contaminata</i> (both varieties), <i>L. dasybotrya</i> , <i>L. dehoopensis</i> , <i>L. elegans</i> var. <i>flava</i> , <i>L. elegans</i> var. <i>membranacea</i> , <i>L. elegans</i> var. <i>suaveolens</i> , <i>L. fasciculata</i> , <i>L. fistulosa</i> , <i>L. framesii</i> , <i>L. gillettii</i> , <i>L. glauca</i> , <i>L. inconspicua</i> , <i>L. isopetala</i> , <i>L. karooica</i> , <i>L. klinghardtiana</i> , <i>L. kliprandensis</i> , <i>L. lactosa</i> , <i>L. leipoldtii</i> , <i>L. liliiflora</i> , <i>L. longibracteata</i> , <i>L. lutea</i> , <i>L. marginata</i> (both subspecies), <i>L. marlothii</i> , <i>L. martinae</i> , <i>L. mathewsii</i> , <i>L. maximiliani</i> , <i>L. mediana</i> (both varieties), <i>L. minima</i> , <i>L. mutabilis</i> , <i>L. namaquensis</i> , <i>L. nardouwensis</i> , <i>L. neilii</i> , <i>L. nordenstamii</i> , <i>L. obscura</i> , <i>L. orchioides</i> (both varieties), <i>L. orthopetala</i> , <i>L. patula</i> , <i>L. physocaulos</i> , <i>L. purpleocaerulea</i> , <i>L. pusilla</i> , <i>L. pustulata</i> , <i>L. reflexa</i> , <i>L. rubida</i> , <i>L. salteri</i> , <i>L. schelpei</i> , <i>L. splendida</i> , <i>L. thomasiae</i> , <i>L. trichophylla</i> (both subspecies), <i>L. undulata</i> (both subspecies), <i>L. unicolor</i> , <i>L. unifolia</i> (both varieties), <i>L. urceolata</i> , <i>L. valeriae</i> , <i>L. variegata</i> , <i>L. ventricosa</i> , <i>L. verticillata</i> , <i>L. violacea</i> , <i>L. viridiflora</i> , <i>L. wiesei</i> , <i>L. zebrina</i> <i>P. ensifolia</i> , <i>P. longituba</i> , <i>P. maughanii</i>

5.18 FRUIT

5.18.1 Results

The fruits of *Lachenalia* were dry, membranous or papyraceous, loculicidal capsules, which dehisced longitudinally. All species were examined and most had ellipsoid capsules. Capsule shape was stable within species and conformed to that of ovary shape except in *L. buchbergensis*, *L. nordenstamii* and *L. zebrina* which had ellipsoid ovaries that subsequently changed their shape and developed into obcordate, broadly winged, aerodynamic capsules, and in *P. ensifolia*, *P. longituba* and *P. maughanii* that had ellipsoid ovaries that developed into ovoid capsules. Capsule size was highly variable across *Lachenalia*, ranging from the minute, obovoid capsules of *L. campanulata* (4 x 3 mm) to the long, ellipsoid capsules of *L. reflexa* (15 x 6 mm). Capsule length was relatively fixed within species.

Four capsule characters were defined for the cladistic analyses:

1) **Capsule shape.** Four states occurred: obovoid (=0); ellipsoid (=1); ovoid (=2) and obcordate (=3). Qualitative character, scored as character 59 (Appendix 1).

The capsules of *Massonia*, and 43 (31%) ingroup taxa (41 *Lachenalia*, two *Polyxena*) were obovoid (Figure 36A). In 90 (65%) *Lachenalia* taxa capsules were ellipsoid (Figure 36B). Three (2%) *Polyxena* taxa had ovoid capsules (Figure 36D), and three (2%) *Lachenalia* taxa had obcordate capsules (Figure 36C, Table 39).

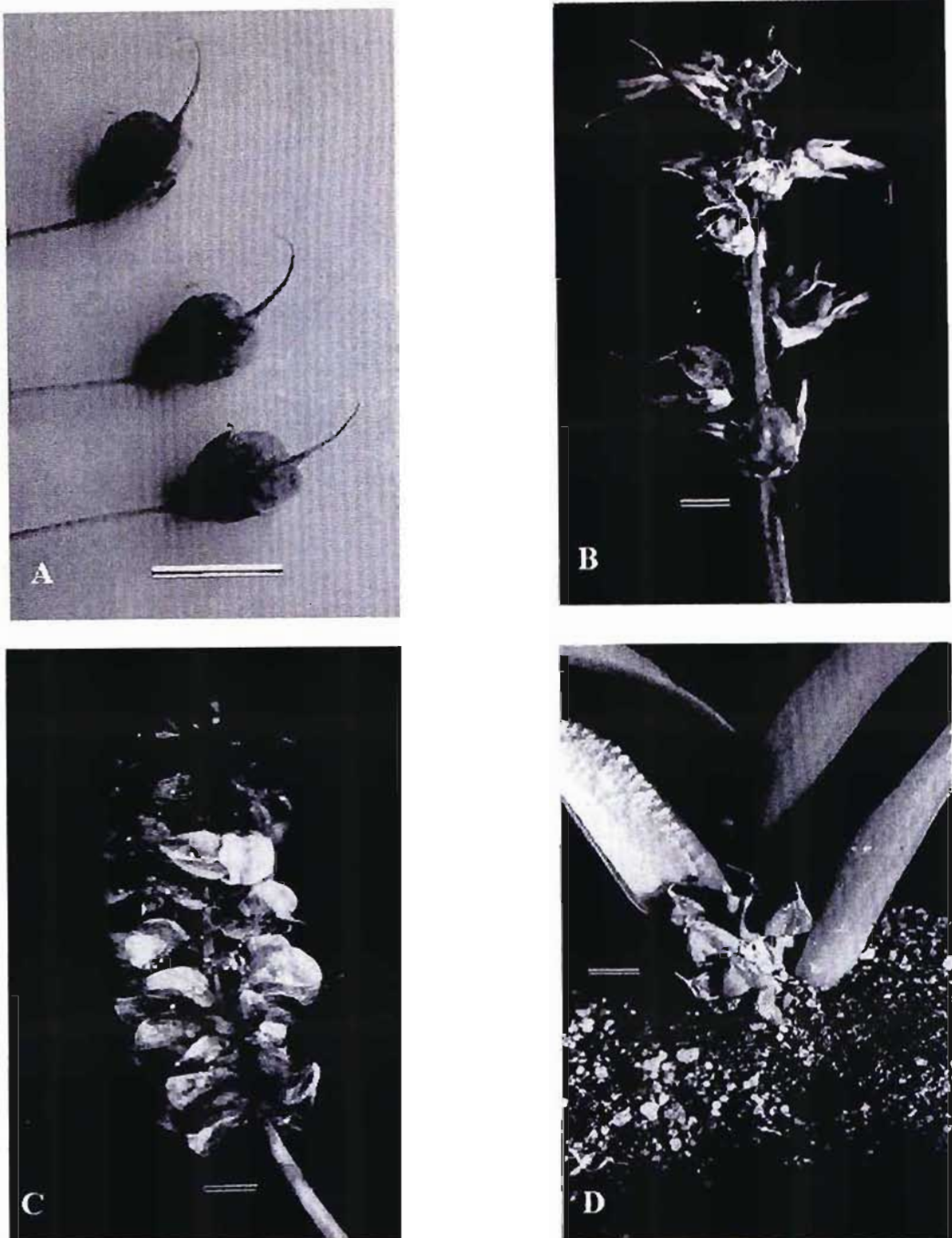


Figure 36. Variation in capsule shape in *Lachenalia* and *Polyxena*.

A, obovoid capsules of *L. anguinea* (Steiner s.n.);

B, ellipsoid capsules of *L. aloides* var. *quadricolor* (Duncan 152); C, obcordate capsules of *L. zebrina*

(Thomas 272); D, ovoid capsules of *P. ensifolia* (Duncan 372).

Scale bars = 10 mm.

Table 39. Variation in capsule shape in <i>Lachenalia</i> , <i>Polyxena</i> and the outgroup <i>Massonia</i>	
Character State	Taxa
Obovoid	<i>L. angelica</i> , <i>L. anguinea</i> , <i>L. arida</i> , <i>L. attenuata</i> , <i>L. bolusii</i> , <i>L. campanulata</i> , <i>L. convallarioides</i> , <i>L. duncanii</i> , <i>L. elegans</i> var. <i>elegans</i> , <i>L. esterhuysenae</i> , <i>L. giessii</i> , <i>L. glaucophylla</i> , <i>L. haarlemensis</i> , <i>L. hirta</i> (both varieties), <i>L. juncifolia</i> (both varieties), <i>L. komsbergensis</i> , <i>L. latimerae</i> , <i>L. leomontana</i> , <i>L. macgregoriorum</i> , <i>L. margaretae</i> , <i>L. moniliformis</i> , <i>L. montana</i> , <i>L. muirii</i> , <i>L. multifolia</i> , <i>L. namibiensis</i> , <i>L. nervosa</i> , <i>L. nutans</i> , <i>L. pearsonii</i> , <i>L. peersii</i> , <i>L. perryae</i> , <i>L. polyphylla</i> , <i>L. polypodantha</i> , <i>L. rosea</i> , <i>L. sargeantii</i> , <i>L. stayneri</i> , <i>L. whitehillensis</i> , <i>L. xerophila</i> , <i>L. youngii</i> , <i>L. zeyheri</i> <i>P. corymbosa</i> , <i>P. paucifolia</i> <i>Massonia</i>
Ellipsoid	<i>L. alba</i> , <i>L. algoensis</i> , <i>L. aloides</i> (all eight varieties), <i>L. ameliae</i> , <i>L. arbutnottiae</i> , <i>L. aurioliae</i> , <i>L. bachmannii</i> , <i>L. barkeriana</i> , <i>L. bowkeri</i> , <i>L. bulbifera</i> , <i>L. canaliculata</i> , <i>L. capensis</i> , <i>L. carnosae</i> , <i>L. cernua</i> , <i>L. comptonii</i> , <i>L. concordiana</i> , <i>L. congesta</i> , <i>L. contaminata</i> (both varieties), <i>L. dasybotrya</i> , <i>L. dehoopensis</i> , <i>L. doleritica</i> , <i>L. elegans</i> var. <i>flava</i> , <i>L. elegans</i> var. <i>membranacea</i> , <i>L. elegans</i> var. <i>suaveolens</i> , <i>L. fasciculata</i> , <i>L. fistulosa</i> , <i>L. framesii</i> , <i>L. gillettii</i> , <i>L. glauca</i> , <i>L. inconspicua</i> , <i>L. isopetala</i> , <i>L. karooica</i> , <i>L. klinghardtiana</i> , <i>L. kliprandensis</i> , <i>L. lactosa</i> , <i>L. leipoldtii</i> , <i>L. liliiflora</i> , <i>L. longibracteata</i> , <i>L. lutea</i> , <i>L. marginata</i> (both subspecies), <i>L. marlothii</i> , <i>L. martiniae</i> , <i>L. mathewsii</i> , <i>L. maximiliani</i> , <i>L. mediana</i> (both varieties), <i>L. minima</i> , <i>L. mutabilis</i> , <i>L. namaquensis</i> , <i>L. nardouwensis</i> , <i>L. neilii</i> , <i>L. obscura</i> , <i>L. orchioides</i> (both varieties), <i>L. orthopetala</i> , <i>L. patula</i> , <i>L. physocaulos</i> , <i>L. purpureocaeerulea</i> , <i>L. pusilla</i> , <i>L. pustulata</i> , <i>L. reflexa</i> , <i>L. rubida</i> , <i>L. salteri</i> , <i>L. schelpei</i> , <i>L. splendida</i> , <i>L. thomasiae</i> , <i>L. trichophylla</i> (both subspecies), <i>L. undulata</i> (both subspecies), <i>L. unicolor</i> , <i>L. unifolia</i> (both varieties), <i>L. urceolata</i> , <i>L. valeriae</i> , <i>L. variegata</i> , <i>L. ventricosa</i> , <i>L. verticillata</i> , <i>L. violacea</i> , <i>L. viridiflora</i> , <i>L. wieseii</i>
Ovoid	<i>P. ensifolia</i> , <i>P. longituba</i> , <i>P. maughanii</i>
Obcordate	<i>L. buchbergensis</i> , <i>L. nordenstamii</i> , <i>L. zebrina</i>

2) **Capsule orientation.** Three states occurred: retains same orientation as flower orientation (=0); bends upwards to suberect position (=1); bends downwards to hanging position (=2). Qualitative character, scored as character 60 (Appendix 1).

In *Massonia* and 109 (78%) ingroup taxa (104 *Lachenalia*, five *Polyxena*) the capsules retained the posture of the flowers. In 29 (21%) *Lachenalia* taxa pedicels bent upwards in fruit to a suberect or erect posture, and in one taxon (*L. multifolia*) the pedicels bent downwards into a hanging position (Table 40).

Character State	Taxa
Retains same orientation as flower orientation	<i>L. alba</i> , <i>L. algoensis</i> , <i>L. ameliae</i> , <i>L. angelica</i> , <i>L. anguinea</i> , <i>L. arbutnotiae</i> , <i>L. arida</i> , <i>L. attenuata</i> , <i>L. aurioliae</i> , <i>L. bachmannii</i> , <i>L. barkeriana</i> , <i>L. bolusii</i> , <i>L. bowkeri</i> , <i>L. buchubergensis</i> , <i>L. bulbifera</i> , <i>L. campanulata</i> , <i>L. canaliculata</i> , <i>L. capensis</i> , <i>L. carnosa</i> , <i>L. cernua</i> , <i>L. comptonii</i> , <i>L. concordiana</i> , <i>L. congesta</i> , <i>L. convallarioides</i> , <i>L. dasybotrya</i> , <i>L. dehoopensis</i> , <i>L. doleritica</i> , <i>L. duncanii</i> , <i>L. elegans</i> (all four varieties), <i>L. esterhuysenae</i> , <i>L. fasciculata</i> , <i>L. fistulosa</i> , <i>L. framesii</i> , <i>L. giessii</i> , <i>L. gillettii</i> , <i>L. glauca</i> , <i>L. glaucophylla</i> , <i>L. haarlemensis</i> , <i>L. inconspicua</i> , <i>L. isopetala</i> , <i>L. juncifolia</i> (both varieties), <i>L. karooica</i> , <i>L. klinghardtiana</i> , <i>L. kliprandensis</i> , <i>L. komsbergensis</i> , <i>L. latimerae</i> , <i>L. leipoldtii</i> , <i>L. liliiflora</i> , <i>L. longibracteata</i> , <i>L. lutea</i> , <i>L. macgregoriorum</i> , <i>L. margaretae</i> , <i>L. marginata</i> (both subspecies), <i>L. marlothii</i> , <i>L. martinae</i> , <i>L. maximiliani</i> , <i>L. minima</i> , <i>L. moniliformis</i> , <i>L. muirii</i> , <i>L. mutabilis</i> , <i>L. namaquensis</i> , <i>L. namibiensis</i> , <i>L. nardouwensis</i> , <i>L. neilii</i> , <i>L. nordenstamii</i> , <i>L. nutans</i> , <i>L. obscura</i> , <i>L. orchioides</i> (both varieties), <i>L. orthopetala</i> , <i>L. patula</i> , <i>L. pearsonii</i> , <i>L. perryae</i> , <i>L. physocaulos</i> , <i>L. pusilla</i> , <i>L. reflexa</i> , <i>L. rubida</i> , <i>L. schelpei</i> , <i>L. splendida</i> , <i>L. stayneri</i> , <i>L. thomasiae</i> , <i>L. trichophylla</i> (both subspecies), <i>L. undulata</i> (both subspecies), <i>L. unicolor</i> , <i>L. unifolia</i> var. <i>schlechteri</i> , <i>L. urceolata</i> , <i>L. valeriae</i> , <i>L. variegata</i> , <i>L. ventricosa</i> , <i>L. verticillata</i> , <i>L. violacea</i> , <i>L. viridiflora</i> , <i>L. whitehillensis</i> , <i>L. wiesei</i> , <i>L. xerophila</i> , <i>L. zebrina</i> , <i>L. zeyheri</i> <i>P. corymbosa</i> , <i>P. ensifolia</i> , <i>P. longituba</i> , <i>P. maughanii</i> , <i>P. paucifolia</i> <i>Massonia</i>
Bends upwards to suberect or erect position	<i>L. aloides</i> (all eight varieties), <i>L. contaminata</i> (both varieties), <i>L. hirta</i> (both varieties), <i>L. lactosa</i> , <i>L. leomontana</i> , <i>L. mathewsii</i> , <i>L. mediana</i> (both varieties), <i>L. montana</i> , <i>L. nervosa</i> , <i>L. peersii</i> , <i>L. polyphylla</i> , <i>L. polypodantha</i> , <i>L. purpureocaerulea</i> , <i>L. pustulata</i> , <i>L. rosea</i> , <i>L. salteri</i> , <i>L. sargeantii</i> , <i>L. unifolia</i> var. <i>unifolia</i> , <i>L. youngii</i>
Bends downwards to hanging position	<i>L. multifolia</i>

3) **Capsule length.** Two discontinuous states occurred: short capsules (=0); and long capsules (=1). Quantitative character, scored as character 61 (Appendix 1).

Massonia and 130 (94%) ingroup taxa (125 *Lachenalia*, all five *Polyxena*) had short capsules up to 10 mm long (Figure 36A, C, D). Capsule length in nine (6%) *Lachenalia* taxa was 14 mm long or longer, *L. aloides* var. *aloides*, *L. aloides* var. *aurea*, *L. aloides* var. *bonaspei*, *L. aloides* var. *piketbergensis*, *L. aloides* var. *quadricolor* (Figure 36B), *L. bulbifera*, *L. reflexa*, *L. rubida* and *L. viridiflora* (Figure 37).

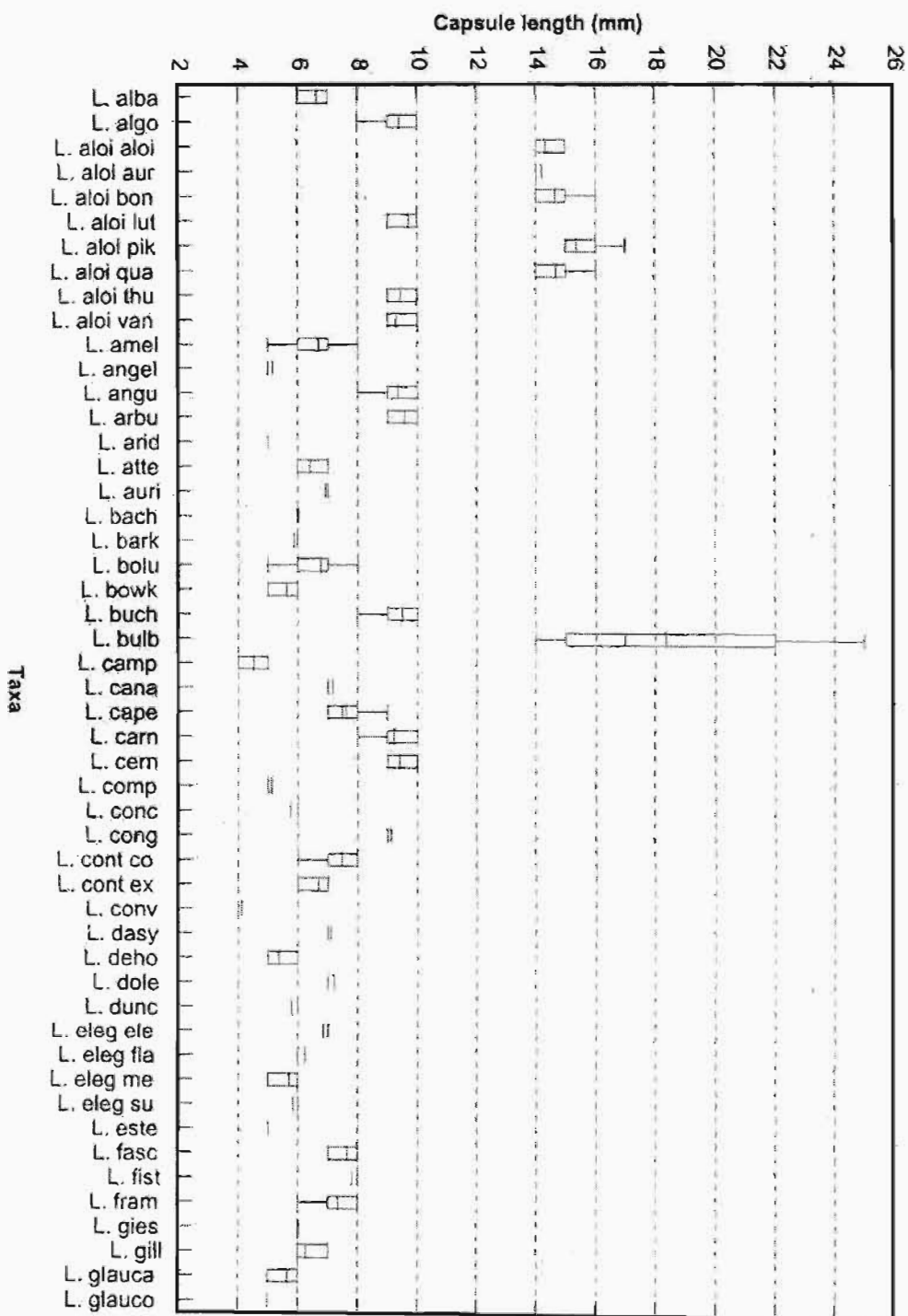


Figure 37. Capsule length in Lachenalia and Polyxena

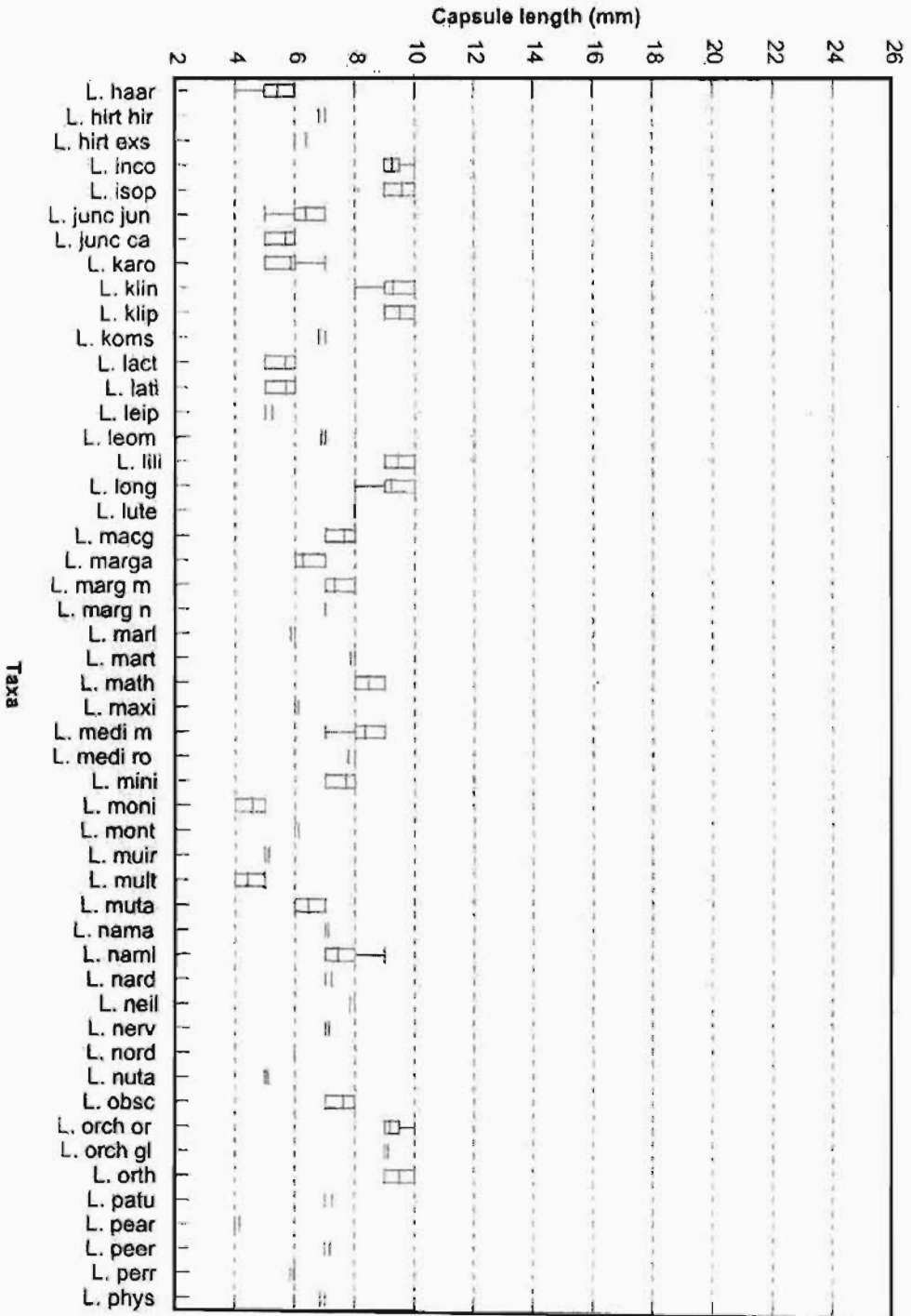


Figure 37. Capsule length in Lachenalia and Polyxena

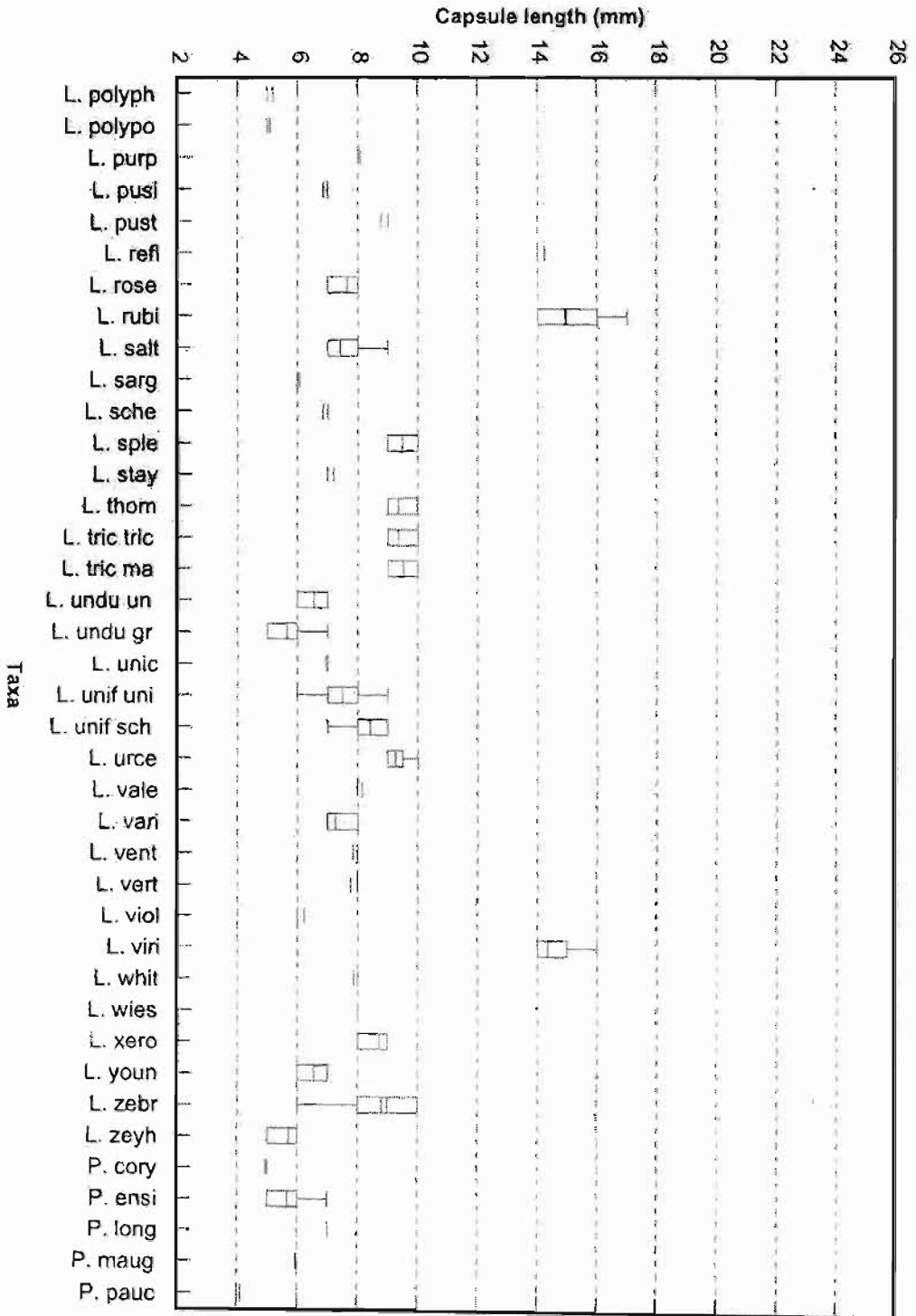


Figure 37. Capsule length in Lichenalia and Polyxena

4) **Infructescence (peduncle) elongation.** Two states occurred: elongated (=0); and non-elongated (=1). Qualitative character, scored as character 62 (Appendix 1).

Massonia and eight (7%) ingroup species (three *Lachenalia*, all five *Polyxena*) had elongated infructescences (peduncles). Immediately before capsule dehiscence, the abbreviated peduncles of these species elongated before falling into a horizontal position. This included five species with subterranean peduncles, *L. barkeriana*, *L. pusilla*, *P. ensifolia*, *P. longituba* and *P. maughanii*, as well as three species with short aerial peduncles, *L. reflexa*, *P. corymbosa* and *P. paucifolia*. In *L. barkeriana*, *L. pusilla*, *P. ensifolia* and *P. maughanii*, the base of the peduncle broke off, allowing the whole infructescence to be carried away by wind, effectively dispersing the seeds over a wide area. In 112 (93%) *Lachenalia* species the peduncle did not elongate in fruit.

5.19 SEED

Jessop (1975) used seed surface characters to form three major tribes (Scilleae, Bowieae and Massonieae) within the Liliaceae *sensu lato*. He placed *Lachenalia* and *Polyxena* into the Massonieae, along with several other genera including *Daubenyia*, *Drimiopsis*, *Eucomis*, *Ledebouria*, *Massonia* and *Veltheimia*, based on seed micromorphology. Wetschnig *et al.* (2002), and Pfosser *et al.* (2003), used seed morphology to delimit most genera of the Massonieae. Seed characters were used as additional diagnostic features in *Lachenalia* by Barker (1978). Müller-Doblies *et al.* (1987) reported that the prominent strophiole of *L. barkeriana* and *L. pusilla* seed acts as an elaiosome, allowing the seed to be dispersed by ants (myrmecochory). The diagnostic characters of seed include shape and size, strophiole length and topography, as well as primary and secondary sculpturing.

5.19.1 Materials and methods

Seed characters such as strophiole size and topography, and primary and secondary sculpturing of the testa were studied by means of light microscopy. Micromorphology of seeds was studied using SEM. Seeds were mounted onto stubs with double-sided tape, sputter-coated with gold-palladium and viewed with a Hitachi S-570 Scanning Electron Microscope at an acceleration voltage of 10kV.

5.19.2 Results

Seed morphology was highly variable across *Lachenalia* but was stable within species. In *Polyxena*, the seed surface of all species was smooth except for *P. corymbosa* which was rugose, whereas in *Lachenalia*, seeds were smooth, rugose, reticulate or colliculate, rarely with conspicuous subrectangular cells c.30-40 x 30 μm (*L. multifolia*). Seeds were black in all *Lachenalia* and *Polyxena* species.

Seed size varied from minute to relatively large. *L. angelica* had the smallest seeds (0.4 x 0.4 mm) and *L. isopetala* had the largest seeds (1.8-2.0 x 1.8-1.9 mm).

The seeds of *Lachenalia* and *Polyxena* had an appendage known as a strophiole that occurred in the micropylar region. Strophiole length was extremely variable across *Lachenalia* but was stable within species. In several species the strophiole was distinctly inflated, providing a useful diagnostic character (Figure 38).

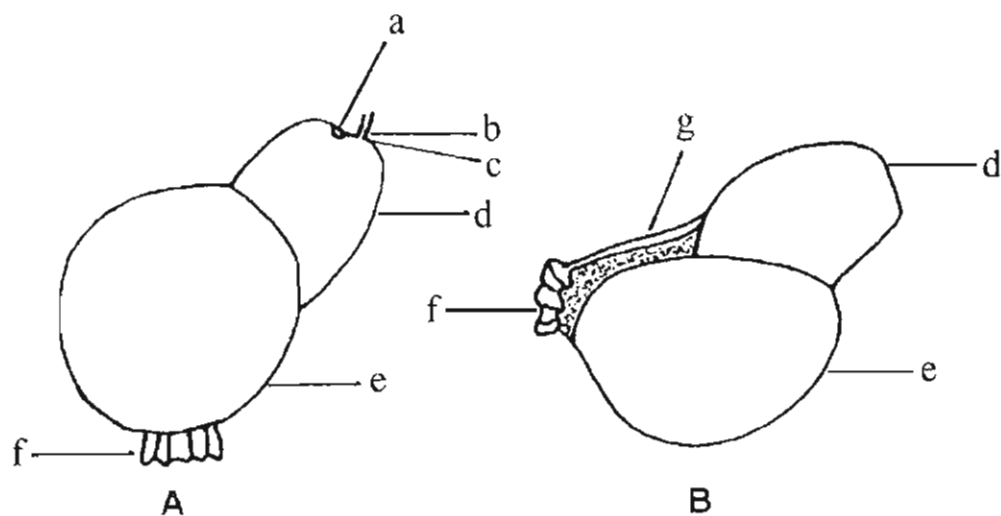


Figure 38. Seed and strophiole morphology in *Lachenalia*. A & B, lateral views of globose seeds of *L. ventricosa* (Duncan 285) X50.

a = micropyle; b = funicle; c = hilum; d = strophiole; e = seed;
f = chalazal collar; g = raphe.

Eleven seed characters were defined for the cladistic analyses:

1) **Testa lustre.** Two states occurred: glossy black (=0); and matte black (=1). Qualitative character, scored as character 63 (Appendix 1).

Seeds of *Massonia* and 86 (72%) ingroup species (84 *Lachenalia*, three *Polyxena*) had a glossy testa. The seeds of 34 (28%) species (32 *Lachenalia*, two *Polyxena*) were matte (Table 41).

Table 41. Variation in testa lustre in <i>Lachenalia</i> , <i>Polyxena</i> and the outgroup <i>Massonia</i>	
Character State	Speices
Glossy black	<p><i>L. algoensis</i>, <i>L. aloides</i> (all eight varieties), <i>L. anguinea</i>, <i>L. arbutnotiae</i>, <i>L. arida</i>, <i>L. bachmannii</i>, <i>L. barkeriana</i>, <i>L. bulbifera</i>, <i>L. campanulata</i>, <i>L. canaliculata</i>, <i>L. capensis</i>, <i>L. carnosae</i>, <i>L. cernua</i>, <i>L. comptonii</i>, <i>L. congesta</i>, <i>L. contaminata</i> (both varieties), <i>L. convallarioides</i>, <i>L. doleritica</i>, <i>L. duncanii</i>, <i>L. elegans</i> (all four varieties), <i>L. esterhuysenae</i>, <i>L. fistulosa</i>, <i>L. framesii</i>, <i>L. giessii</i>, <i>L. gillettii</i>, <i>L. glauca</i>, <i>L. glaucophylla</i>, <i>L. haarlemensis</i>, <i>L. isopetala</i>, <i>L. juncifolia</i> (both varieties), <i>L. karooica</i>, <i>L. klinghardtiana</i>, <i>L. kliprandensis</i>, <i>L. lactosa</i>, <i>L. latimeriae</i>, <i>L. leipoldtii</i>, <i>L. leomontana</i>, <i>L. liliiflora</i>, <i>L. longibracteata</i>, <i>L. lutea</i>, <i>L. margaretae</i>, <i>L. marginata</i> (both subspecies), <i>L. marlothii</i>, <i>L. martinae</i>, <i>L. mathewsii</i>, <i>L. maximiliani</i>, <i>L. mediana</i> (both varieties), <i>L. minima</i>, <i>L. moniliformis</i>, <i>L. muirii</i>, <i>L. multifolia</i>, <i>L. mutabilis</i>, <i>L. namaquensis</i>, <i>L. namibiensis</i>, <i>L. nardouwensis</i>, <i>L. nervosa</i>, <i>L. nutans</i>, <i>L. obscura</i>, <i>L. orchioides</i> (both varieties), <i>L. orthopetala</i>, <i>L. pearsonii</i>, <i>L. peersii</i>, <i>L. physocaulos</i>, <i>L. purpureocaerulea</i>, <i>L. pusilla</i>, <i>L. pustulata</i>, <i>L. reflexa</i>, <i>L. rosea</i>, <i>L. rubida</i>, <i>L. salteri</i>, <i>L. splendida</i>, <i>L. stayneri</i>, <i>L. thomasiae</i>, <i>L. unicolor</i>, <i>L. unifolia</i> (both varieties), <i>L. urceolata</i>, <i>L. valeriae</i>, <i>L. variegata</i>, <i>L. ventricosa</i>, <i>L. violacea</i>, <i>L. xerophila</i>, <i>L. youngii</i>, <i>L. zeyheri</i> <i>P. ensifolia</i>, <i>P. longituba</i>, <i>P. maughanii</i> <i>Massonia</i></p>
Matte black	<p><i>L. alba</i>, <i>L. ameliae</i>, <i>L. angelica</i>, <i>L. attenuata</i>, <i>L. aurioliae</i>, <i>L. bolusii</i>, <i>L. bowkeri</i>, <i>L. buchbergensis</i>, <i>L. concordiana</i>, <i>L. dasybotrya</i>, <i>L. dehoopensis</i>, <i>L. fasciculata</i>, <i>L. hirta</i> (both varieties), <i>L. inconspicua</i>, <i>L. komsbergensis</i>, <i>L. macgregoriorum</i>, <i>L. montana</i>, <i>L. neilii</i>, <i>L. nordenstamii</i>, <i>L. patula</i>, <i>L. perryae</i>, <i>L. polyphylla</i>, <i>L. polypodantha</i>, <i>L. sargeantii</i>, <i>L. schelpei</i>, <i>L. trichophylla</i> (both subspecies), <i>L. undulata</i> (both subspecies), <i>L. verticillata</i>, <i>L. viridiflora</i>, <i>L. whitehillensis</i>, <i>L. wiesei</i>, <i>L. zebrina</i> <i>P. corymbosa</i>, <i>P. paucifolia</i></p>

2) **Seed length.** Three discontinuous states occurred: medium length seeds (=0); short seeds (=1); and long seeds (=2). Quantitative character, scored as character 64 (Appendix 1).

Massonia and 107 (89%) ingroup species (102 *Lachenalia*, all five *Polyxena*) had medium length seeds 0.9-1.4 mm long. Four (3%) *Lachenalia* species had short seeds 0.4-0.5 mm long, *L. angelica*, *L. muirii*, *L. patula* and *L. trichophylla* (both subspecies). Nine (8%) *Lachenalia* species had long seeds 1.8 mm long or longer, *L. buchbergensis*, *L. congesta*, *L. doleritica*, *L. isopetala*, *L. nordenstamii*, *L. pearsonii*, *L. schelpei*, *L. xerophila* and *L. zebrina* (Figure 39, Table 42). The longest seeds were those of *L. buchbergensis* which were distinctly longer than broad at 3.0-3.5 x 1.0-1.1 mm.

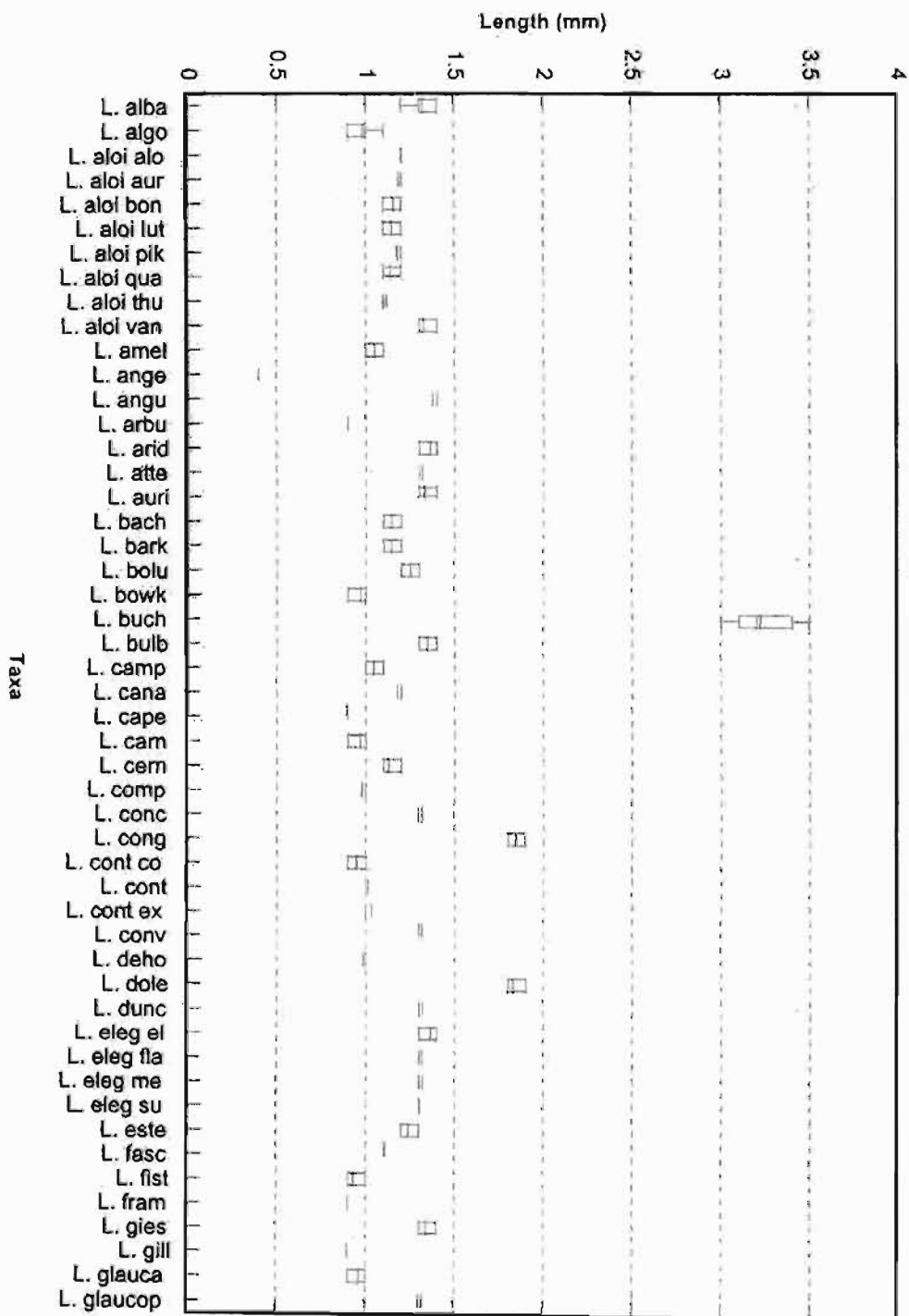


Figure 39. Seed length in Lachenalia and Polyxena

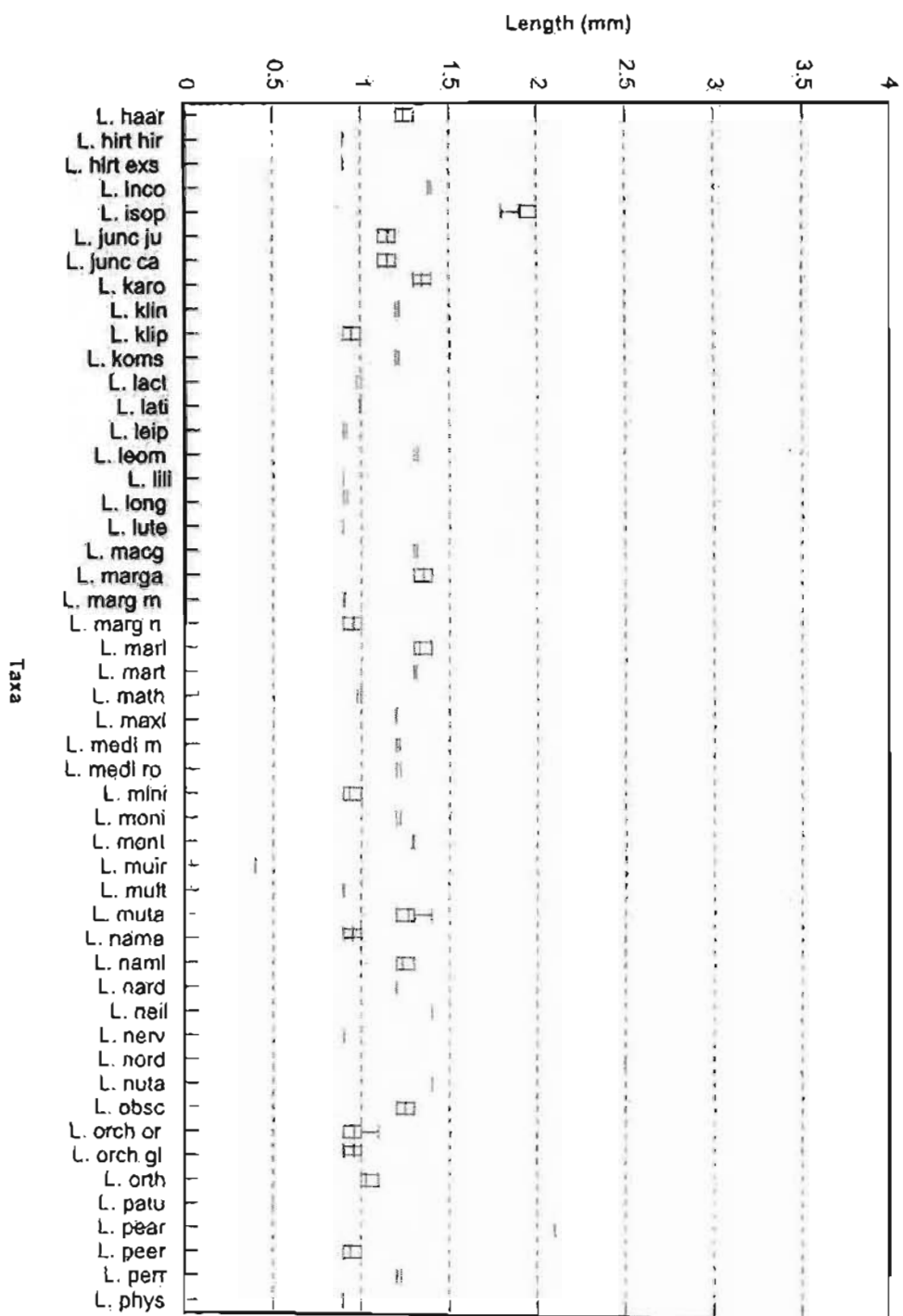


Figure 39. Seed length in *Lachenalia* and *Polyxena*

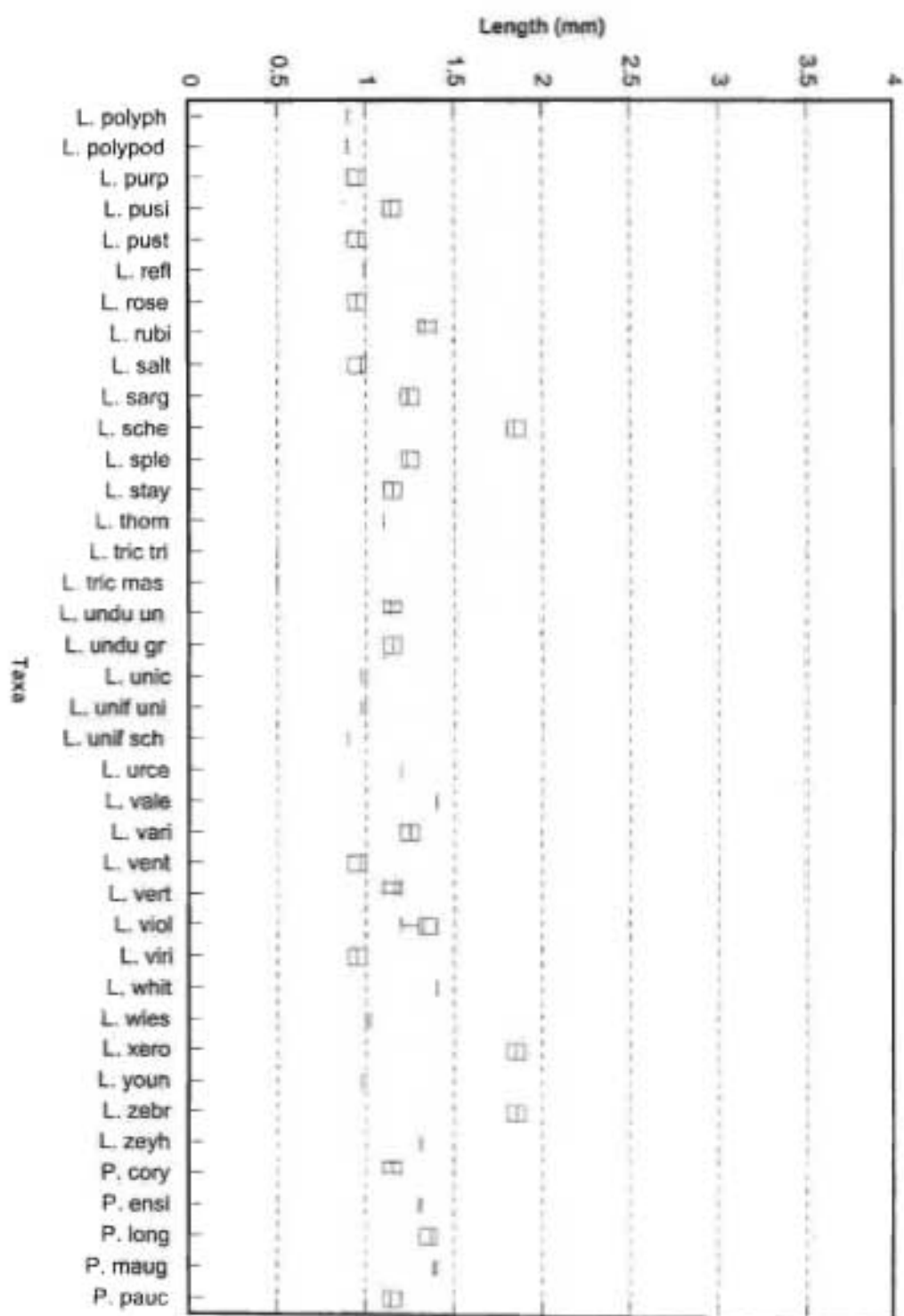


Figure 39. Seed length in *Lachenalia* and *Polyxena*

3) **Seed width.** Three discontinuous states occurred: medium width seeds (=0); narrow seeds (=1); and wide seeds (=2). Quantitative character, scored as character 65 (Appendix 1).

Massonia and 105 (88%) ingroup species (100 *Lachenalia*, all five *Polyxena*) had medium width seeds 0.8-1.4 mm wide. Five (4%) *Lachenalia* species had narrow seeds 0.4-0.5 mm wide, *L. angelica*, *L. muirii*, *L. patula*, *L. polyphylla* and *L. trichophylla* (both subspecies). Ten (8%) *Lachenalia* species had wide seeds 1.8 mm wide or wider, *L. anguinea*, *L. arida*, *L. congesta*, *L. doleritica*, *L. giessii*, *L. isopetala*, *L. marlothii*, *L. neilii*, *L. pearsonii* and *L. zebrina* (Figure 40, Table 42).

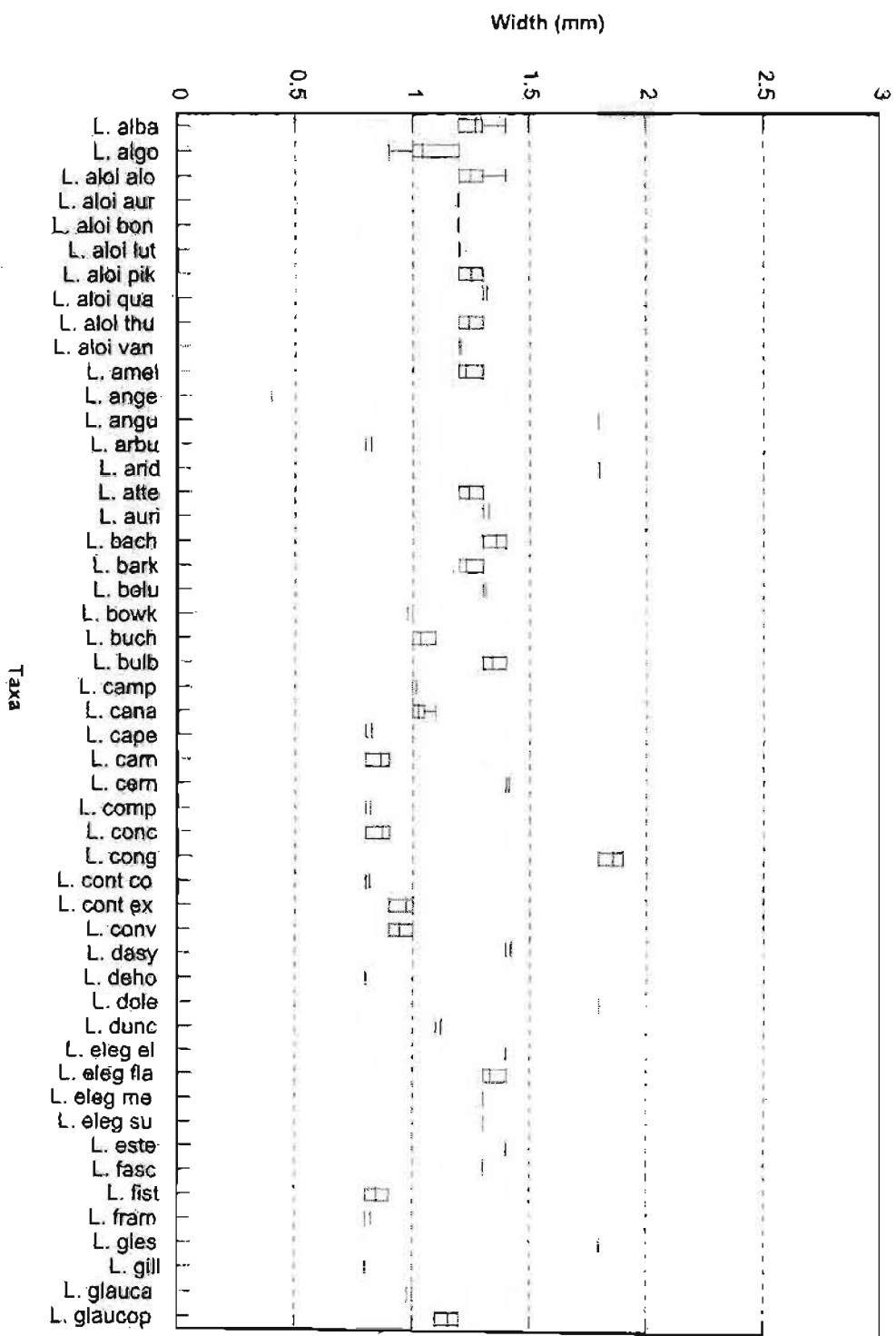


Figure 40. Seed width in Lichenalia and Polyxena

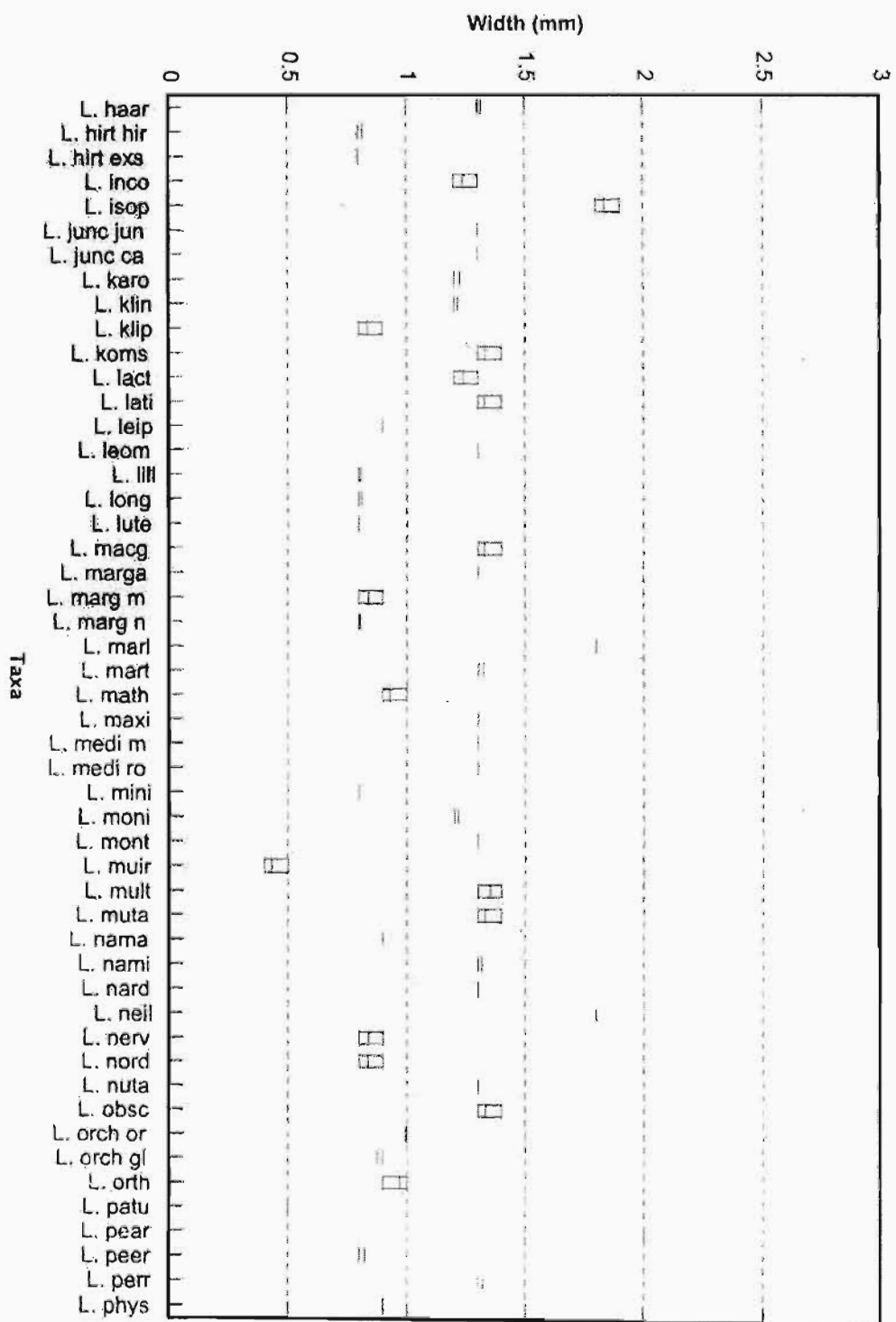


Figure 40. Seed width in Lachenalia and Polyxena

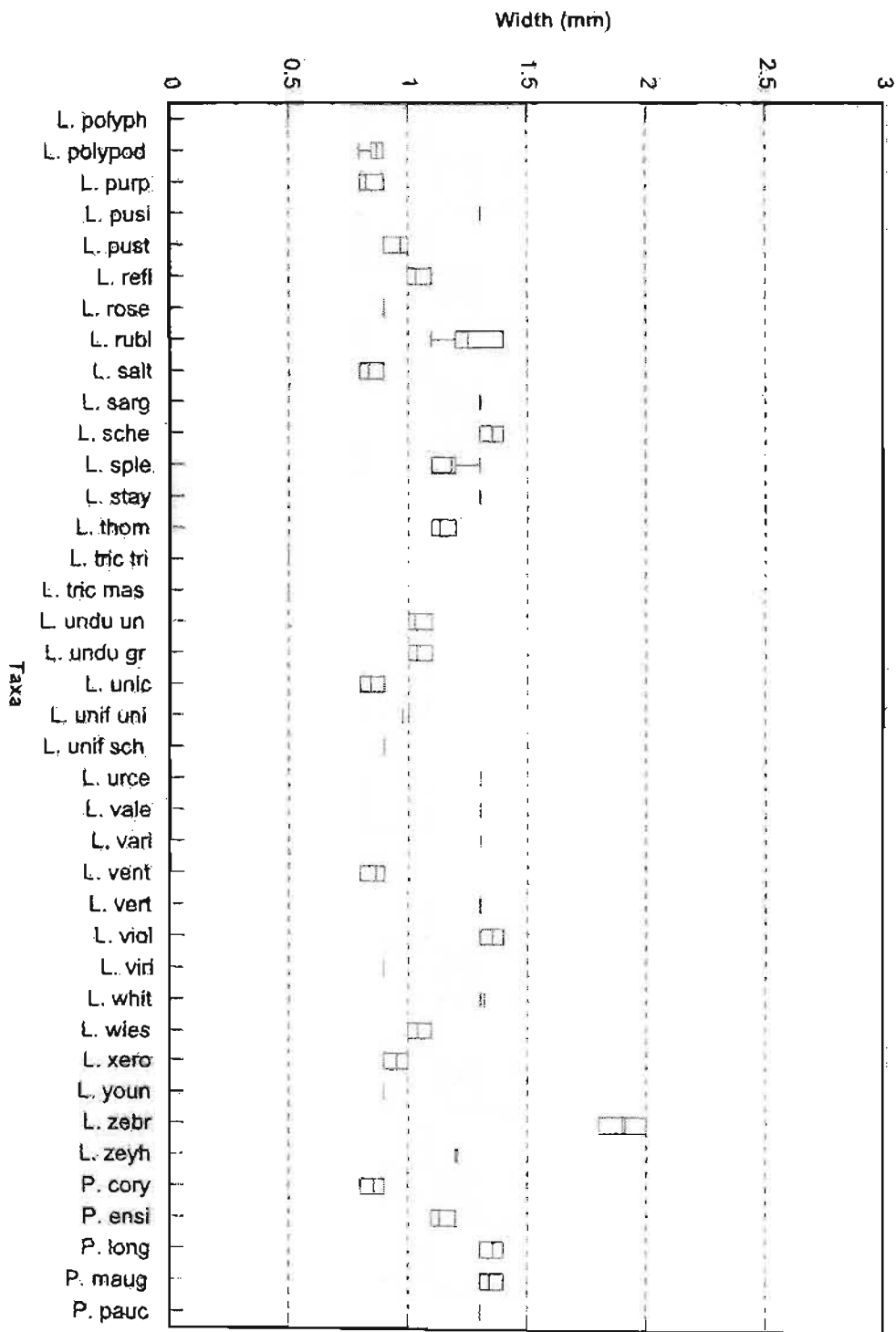


Figure 40. Seed width in Lichenalia and Polyxena

4) **Seed shape.** Three states occurred: globose (=0); ovoid, in which the girth of the seed was less than that of the length (=1); and oblong, in which the length of the seed was more than three times the girth, with the sides almost parallel (=2). Qualitative character, scored as character 66 (Appendix 1).

Massonia and 78 (65%) ingroup species (77 *Lachenalia*, one *Polyxena*) had globose seeds (Figure 41A-C). In 39 (32.5%) *Lachenalia* and *Polyxena* species (35 *Lachenalia*, four *Polyxena*) seed shape was ovoid (Figure 41D, E), and in three (2.5%) *Lachenalia* species (*L. buchbergensis*, *L. nordenstamii* and *L. xerophila*) the seeds were oblong (Figure 41F, Table 42).

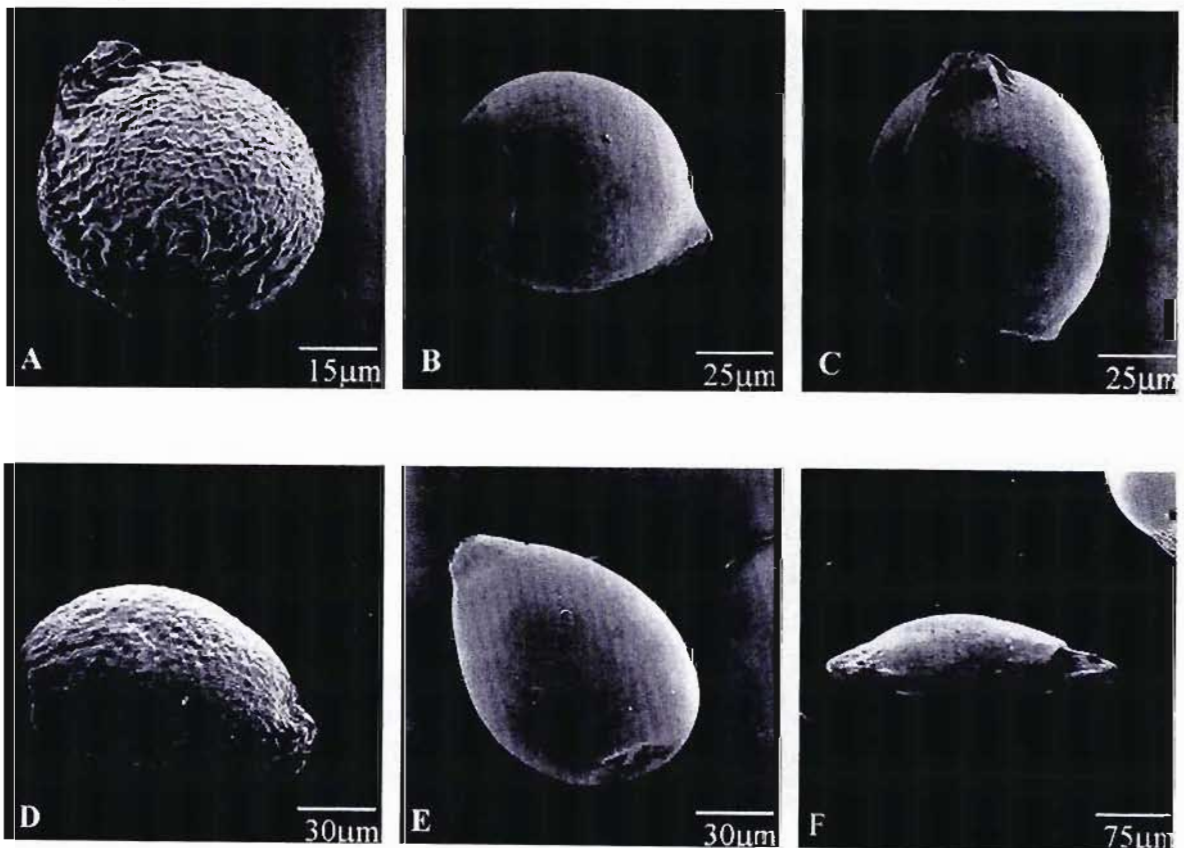


Figure 41. Scanning electron micrographs illustrating variation in seed shape in *Lachenalia* and *Polyxena*. Globose seeds of A, *L. trichophylla* subsp. *trichophylla* (Thomas 96); B, *L. comptonii* (Duncan 107); C, *L. juncifolia* var. *juncifolia* (Bohnen 8495). Ovoid seeds of D, *P. corymbosa* (Simmons s.n.); E, *P. ensifolia* (Duncan 372). Oblong seed of F, *L. nordenstamii* (Nordenstam 1762).

Table 42. Variation in seed and strophiole characters in *Lachenalia*, *Polyxena* and the outgroup *Massonia*

TAXA	SEED	TESTA		SEED	STROPHIOLE	
	shape	primary sculpturing	secondary sculpturing	size in mm	length in mm	surface texture
<i>L. alba</i>	ovoid	smooth	absent	1.2-1.4 x 1.2-1.4	0.5-0.6	ridged
<i>L. algoensis</i>	globose	smooth	absent	0.9-1.1 x 0.9-1.2	1.1-1.2	smooth
<i>L. aloides</i> var. <i>aloides</i>	globose	smooth	absent	1.1-1.3 x 1.2-1.4	1.1-1.2	smooth
<i>L. aloides</i> var. <i>aurea</i>	globose	smooth	absent	1.1-1.3 x 1.1-1.3	1.1-1.2	smooth
<i>L. aloides</i> var. <i>bonaspei</i>	globose	smooth	absent	1.1-1.2 x 1.1-1.3	1.1-1.2	smooth
<i>L. aloides</i> var. <i>luteola</i>	globose	smooth	absent	1.1-1.2 x 1.2-1.3	1.1-1.2	smooth
<i>L. aloides</i> var. <i>piketbergensis</i>	globose	smooth	absent	1.1-1.2 x 1.2-1.3	1.1-1.2	smooth
<i>L. aloides</i> var. <i>quadricolor</i>	globose	smooth	absent	1.1-1.2 x 1.3-1.4	1.1-1.2	smooth
<i>L. aloides</i> var. <i>thunbergii</i>	globose	smooth	absent	1.1-1.2 x 1.2-1.3	1.1-1.2	smooth
<i>L. aloides</i> var. <i>vanzyliae</i>	globose	smooth	absent	1.3-1.4 x 1.2-1.3	1.4-1.5	smooth
<i>L. ameliae</i>	ovoid	smooth	absent	1.0-1.1 x 1.2-1.3	0.5-0.6	ridged
<i>L. angelica</i>	globose	smooth	reticulate	0.4 x 0.4	0.1-0.2	ridged
<i>L. anguinea</i>	globose	smooth	absent	1.3-1.4 x 1.8	0.1-0.2	ridged
<i>L. arbuthnotiae</i>	globose	smooth	absent	0.9 x 0.8-0.9	0.7-0.8	smooth
<i>L. arida</i>	globose	smooth	absent	1.3-1.4 x 1.8	0.2-0.3	ridged
<i>L. attenuata</i>	ovoid	smooth	absent	1.3-1.4 x 1.2-1.3	1.1	ridged
<i>L. aurioliae</i>	ovoid	smooth	absent	1.3-1.4 x 1.3-1.4	1.1	ridged
<i>L. bachmannii</i>	globose	smooth	absent	1.1-1.2 x 1.3-1.4	0.3	ridged
<i>L. barkeriana</i>	globose	smooth	absent	1.1-1.2 x 1.2-1.3	0.6-0.7	smooth
<i>L. bolusii</i>	globose	rugose	absent	1.2-1.3 x 1.3-1.4	0.6-0.7	smooth
<i>L. bowkeri</i>	globose	smooth	reticulate	0.9-1.0 x 0.9-1.0	0.6-0.7	ridged
<i>L. buchbergensis</i>	oblong	rugose	absent	3.0-3.5 x 1.0-1.1	0.3	ridged
<i>L. bulbifera</i>	globose	smooth	absent	1.3-1.4 x 1.3-1.4	1.4-1.6	smooth
<i>L. campanulata</i>	globose	smooth	absent	1.0-1.1 x 1.0-1.1	0.1-0.2	ridged
<i>L. canaliculata</i>	ovoid	smooth	absent	1.1-1.2 x 1.0-1.1	0.7-0.8	ridged

Table 42. Variation in seed and strophiole characters in *Lachenalia*, *Polyxena* and the outgroup *Massonia*

TAXA	SEED	TESTA		SEED	STROPHIOLE	
	shape	primary sculpturing	secondary sculpturing	size in mm	length in mm	surface texture
<i>L. capensis</i>	globose	smooth	absent	0.9 x 0.8-0.9	0.7-0.8	smooth
<i>L. carnosa</i>	ovoid	smooth	absent	0.9-1.0 x 0.8-0.9	0.1-0.2	ridged
<i>L. cernua</i>	globose	smooth	absent	1.1-1.2 x 1.4	1.1	smooth
<i>L. comptonii</i>	globose	smooth	absent	0.9-1.0 x 0.8-0.9	0.1-0.2	ridged
<i>L. concordiana</i>	ovoid	smooth	absent	1.3-1.4 x 0.8-0.9	0.8	ridged
<i>L. congesta</i>	globose	smooth	absent	1.8-1.9 x 1.8-1.9	0.1	ridged
<i>L. contaminata</i> var. <i>contaminata</i>	globose	smooth	absent	0.9-1.0 x 0.8-0.9	0.1-0.2	ridged
<i>L. contaminata</i> var. <i>exserta</i>	globose	smooth	absent	1.0-1.1 x 0.9-1.0	0.1-0.2	ridged
<i>L. convallarioides</i>	globose	smooth	absent	0.9-1.2 x 0.9-1.0	0.1-0.2	ridged
<i>L. dasybotrya</i>	ovoid	smooth	absent	1.3-1.4 x 1.4	0.5	ridged
<i>L. dehoopensis</i>	globose	smooth	reticulate	0.9-1.0 x 0.8	0.6-0.7	ridged
<i>L. doleritica</i>	ovoid	smooth	absent	1.8-1.9 x 1.8	1.1-1.2	ridged
<i>L. duncanii</i>	ovoid	smooth	absent	1.3-1.4 x 1.1-1.2	0.6-0.7	ridged
<i>L. elegans</i> var. <i>elegans</i>	globose	smooth	absent	1.3-1.4 x 1.4	0.8	smooth
<i>L. elegans</i> var. <i>flava</i>	globose	smooth	absent	1.3-1.4 x 1.3-1.4	0.7-0.8	smooth
<i>L. elegans</i> var. <i>membranacea</i>	globose	smooth	absent	1.3-1.4 x 1.3	0.8	smooth
<i>L. elegans</i> var. <i>suaveolens</i>	globose	smooth	absent	1.3-1.4 x 1.3	0.8	smooth
<i>L. esterhuysenae</i>	globose	smooth	absent	1.2-1.3 x 1.4	0.1-0.2	ridged
<i>L. fasciculata</i>	ovoid	smooth	absent	1.1-1.2 x 1.3	0.6-0.7	ridged
<i>L. fistulosa</i>	globose	smooth	absent	0.9-1.0 x 0.8-0.9	0.6-0.7	smooth
<i>L. framesii</i>	ovoid	smooth	reticulate	0.9 x 0.8-0.9	0.1-0.2	ridged
<i>L. giessii</i>	globose	smooth	absent	1.3-1.4 x 1.8	0.1	ridged
<i>L. gillettii</i>	globose	smooth	absent	0.9-1.0 x 0.8	0.1	ridged
<i>L. glauca</i>	globose	smooth	reticulate	0.9-1.0 x 0.9-1.0	0.5-0.6	smooth
<i>L. glaucophylla</i>	ovoid	smooth	absent	1.3-1.4 x 1.1-1.2	0.8	ridged

Table 42. Variation in seed and strophiole characters in *Lachenalia*, *Polyxena* and the outgroup *Massonia*

TAXA	SEED	TESTA		SEED	STROPHIOLE	
	shape	primary sculpturing	secondary sculpturing	size in mm	length in mm	surface texture
<i>L. haarlemensis</i>	globose	smooth	absent	1.2-1.3 x 1.3-1.4	0.5-0.6	ridged
<i>L. hirta</i> var. <i>hirta</i>	globose	smooth	reticulate	0.9 x 0.8-0.9	0.1	ridged
<i>L. hirta</i> var. <i>exserta</i>	globose	smooth	reticulate	0.9 x 0.8	0.1	ridged
<i>L. inconspicua</i>	ovoid	smooth	reticulate	1.3-1.4 x 1.2-1.3	1.1	ridged
<i>L. isopetala</i>	globose	smooth	absent	1.8-2.0 x 1.8-1.9	0.1	ridged
<i>L. juncifolia</i> var. <i>juncifolia</i>	globose	smooth	absent	1.1-1.2 x 1.3	0.2	ridged
<i>L. juncifolia</i> var. <i>campanulata</i>	globose	smooth	absent	1.1-1.2 x 1.3	0.2	ridged
<i>L. karooica</i>	ovoid	smooth	reticulate	1.3-1.4 x 1.2-1.3	1.1	ridged
<i>L. klinghardtiana</i>	globose	smooth	absent	1.2-1.3 x 1.2-1.3	0.5-0.6	ridged
<i>L. kliprandensis</i>	ovoid	smooth	absent	0.9-1.0 x 0.8-0.9	0.5	ridged
<i>L. komsbergensis</i>	globose	rugose	absent	1.2-1.3 x 1.3-1.4	0.5-0.6	ridged
<i>L. lactosa</i>	globose	smooth	absent	0.9-1.0 x 1.2-1.3	0.5	smooth
<i>L. latimerae</i>	globose	smooth	absent	0.9-1.0 x 1.3-1.4	0.6	ridged
<i>L. leipoldtii</i>	globose	smooth	absent	0.9-1.0 x 0.9	0.5	smooth
<i>L. leomontana</i>	globose	smooth	absent	1.3-1.4 x 1.3	0.5-0.6	smooth
<i>L. liliiflora</i>	ovoid	smooth	absent	0.9 x 0.8-0.9	0.2	ridged
<i>L. longibracteata</i>	globose	smooth	absent	0.9-1.0 x 0.8-0.9	0.8	smooth
<i>L. lutea</i>	globose	smooth	absent	0.9 x 0.8	0.5-0.6	smooth
<i>L. macgregoriorum</i>	globose	smooth	absent	1.3-1.4 x 1.3-1.4	0.1	ridged
<i>L. margaretae</i>	globose	smooth	absent	1.3-1.4 x 1.3	0.6	smooth
<i>L. marginata</i> subsp. <i>marginata</i>	globose	smooth	absent	0.9-1.0 x 0.8-0.9	0.6-0.7	smooth
<i>L. marginata</i> subsp. <i>neglecta</i>	globose	smooth	absent	0.9-1.0 x 0.8-0.9	0.6-0.7	smooth
<i>L. marlothii</i>	ovoid	smooth	absent	1.3-1.4 x 1.8	1.1	ridged
<i>L. martinae</i>	globose	smooth	absent	1.3-1.4 x 1.3-1.4	0.8	smooth
<i>L. mathewsii</i>	ovoid	smooth	absent	0.9-1.0 x 0.9-1.0	0.2	ridged

Table 42. Variation in seed and strophiole characters in <i>Lachenalia</i> , <i>Polyxena</i> and the outgroup <i>Massonia</i>						
TAXA	SEED	TESTA		SEED	STROPHIOLE	
	shape	primary sculpturing	secondary sculpturing	size in mm	length in mm	surface texture
<i>L. maximiliani</i>	ovoid	smooth	absent	1.2 x 1.3	0.6	ridged
<i>L. mediana</i> var. <i>mediana</i>	globose	smooth	absent	1.2-1.3 x 1.3	1.1-1.2	smooth
<i>L. mediana</i> var. <i>rogersii</i>	globose	smooth	absent	1.2 x 1.3	1.1	smooth
<i>L. minima</i>	ovoid	smooth	absent	0.9-1.0 x 0.8	0.6-0.7	ridged
<i>L. moniliformis</i>	globose	smooth	absent	1.2-1.3 x 1.2-1.3	0.3	ridged
<i>L. montana</i>	globose	smooth	colliculate	1.2-1.3 x 1.3	0.1	ridged
<i>L. muirii</i>	globose	smooth	absent	0.4 x 0.4-0.5	0.5	smooth
<i>L. multifolia</i>	globose	smooth	absent	0.9 x 1.3-1.4	0.1-0.2	ridged
<i>L. mutabilis</i>	globose	smooth	absent	1.2-1.4 x 1.3-1.4	0.6-0.7	smooth
<i>L. namaquensis</i>	ovoid	smooth	reticulate	0.9-1.0 x 0.9	0.5	ridged
<i>L. namibiensis</i>	globose	smooth	absent	1.2-1.3 x 1.3-1.4	0.1	ridged
<i>L. nardouwensis</i>	globose	smooth	absent	1.2 x 1.3	0.6-0.7	smooth
<i>L. neilii</i>	ovoid	smooth	absent	1.4 x 1.8	0.6	ridged
<i>L. nervosa</i>	globose	smooth	absent	0.9 x 0.8-0.9	0.6-0.7	smooth
<i>L. nordenstamii</i>	oblong	smooth	absent	2.5 x 0.8-0.9	0.3	ridged
<i>L. nutans</i>	globose	smooth	absent	1.4 x 1.3	0.2	ridged
<i>L. obscura</i>	ovoid	smooth	absent	1.2-1.3 x 1.3-1.4	0.6-0.7	ridged
<i>L. orchioides</i> var. <i>orchioides</i>	globose	smooth	absent	0.9-1.1 x 0.9-1.1	0.7-0.8	smooth
<i>L. orchioides</i> var. <i>glaucina</i>	globose	smooth	absent	0.9-1.0 x 0.8-0.9	0.7-0.8	smooth
<i>L. orthopetala</i>	ovoid	smooth	absent	1.0-1.1 x 0.9-1.0	0.2-0.3	ridged
<i>L. patula</i>	globose	rugose	absent	0.5 x 0.5	0.2-0.3	ridged
<i>L. pearsonii</i>	globose	smooth	absent	2.1 x 2.0	0.1-0.2	ridged
<i>L. peersii</i>	globose	smooth	absent	0.9-1.0 x 0.8-0.9	0.6-0.7	smooth
<i>L. perryae</i>	ovoid	smooth	reticulate	1.2-1.3 x 1.3-1.4	0.5	ridged
<i>L. physocaulos</i>	globose	smooth	absent	0.9 x 0.9	0.5	smooth

Table 42. Variation in seed and strophiole characters in *Lachenalia*, *Polyxena* and the outgroup *Massonia*

TAXA	SEED	TESTA		SEED	STROPHIOLE	
	shape	primary sculpturing	secondary sculpturing	size in mm	length in mm	surface texture
<i>L. polyphylla</i>	globose	rugose	absent	0.9 x 0.5	0.2	ridged
<i>L. polypodantha</i>	globose	smooth	reticulate	0.9 x 0.8-0.9	0.2-0.3	ridged
<i>L. purpureocaerulea</i>	globose	smooth	absent	0.9-1.0 x 0.8-0.9	0.2-0.3	ridged
<i>L. pusilla</i>	globose	smooth	absent	1.1-1.2 x 1.3	0.6-0.7	smooth
<i>L. pustulata</i>	globose	smooth	absent	0.9-1.0 x 0.9-1.0	0.1-0.2	ridged
<i>L. reflexa</i>	globose	smooth	absent	0.9-1.1 x 1.0-1.1	0.6-0.7	smooth
<i>L. rosea</i>	globose	smooth	absent	0.9-1.0 x 0.9	0.7-0.8	smooth
<i>L. rubida</i>	globose	smooth	absent	1.3-1.4 x 1.2-1.4	0.8	smooth
<i>L. salteri</i>	globose	smooth	absent	0.9-1.0 x 0.8-0.9	0.6-0.7	smooth
<i>L. sargeantii</i>	globose	smooth	colliculate	1.2-1.3 x 1.3	0.2-0.3	ridged
<i>L. schelpei</i>	ovoid	smooth	absent	1.8-1.9 x 1.3-1.4	1.2	ridged
<i>L. splendida</i>	ovoid	smooth	absent	1.1-1.2 x 1.1-1.3	0.3	ridged
<i>L. stayneri</i>	globose	smooth	absent	1.1-1.2 x 1.3	0.8	smooth
<i>L. thomasiae</i>	globose	smooth	absent	1.1 x 1.1-1.2	0.8	smooth
<i>L. trichophylla</i> subsp. <i>trichophylla</i>	globose	smooth	reticulate	0.5 x 0.5	0.1	ridged
<i>L. trichophylla</i> subsp. <i>massonii</i>	globose	smooth	reticulate	0.5 x 0.5	0.1	ridged
<i>L. undulata</i> subsp. <i>undulata</i>	ovoid	smooth	absent	1.1-1.2 x 1.0-1.1	0.5-0.6	ridged
<i>L. undulata</i> subsp. <i>grandifolia</i>	ovoid	smooth	absent	1.1-1.2 x 1.0-1.1	0.5	ridged
<i>L. unicolor</i>	globose	smooth	absent	0.9-1.0 x 0.8-0.9	0.1	ridged
<i>L. unifolia</i> var. <i>unifolia</i>	globose	smooth	absent	0.9-1.0 x 0.9-1.0	0.1	ridged
<i>L. unifolia</i> var. <i>schlechteri</i>	globose	smooth	absent	0.9 x 0.9	0.1	ridged
<i>L. urceolata</i>	globose	smooth	absent	1.2 x 1.3	0.6-0.7	ridged
<i>L. valeriae</i>	ovoid	smooth	absent	1.4 x 1.3	0.2-0.3	ridged
<i>L. variegata</i>	globose	smooth	absent	1.2-1.3 x 1.3	1.1	smooth
<i>L. ventricosa</i>	ovoid	smooth	absent	0.9-1.0 x 0.8-0.9	0.7-0.8	smooth

Table 42. Variation in seed and strophiole characters in *Lachenalia*, *Polyxena* and the outgroup *Massonia*

TAXA	SEED	TESTA		SEED	STROPHIOLE	
	shape	primary sculpturing	secondary sculpturing	size in mm	length in mm	surface texture
<i>L. verticillata</i>	ovoid	smooth	absent	1.1-1.2 x 1.3	0.6-0.7	ridged
<i>L. violacea</i>	globose	smooth	absent	1.2-1.4 x 1.3-1.4	0.7-0.8	smooth
<i>L. viridiflora</i>	globose	smooth	absent	0.9-1.0 x 0.9	0.7-0.8	smooth
<i>L. whitehillensis</i>	ovoid	smooth	absent	1.4 x 1.3-1.4	0.5-0.6	ridged
<i>L. wiesei</i>	ovoid	rugose	absent	1.0-1.1 x 1.0-1.1	0.5	ridged
<i>L. xerophila</i>	oblong	smooth	absent	1.8-1.9 x 0.9-1.0	0.3	ridged
<i>L. youngii</i>	globose	smooth	absent	0.9-1.0 x 0.9	0.6	smooth
<i>L. zebrina</i>	ovoid	smooth	absent	1.8-1.9 x 1.8-2.0	0.5-0.6	ridged
<i>L. zeyheri</i>	globose	smooth	absent	1.3-1.4 x 1.2-1.3	0.1-0.2	ridged
<i>P. corymbosa</i>	ovoid	rugose	absent	1.1-1.2 x 0.8-0.9	0.2	ridged
<i>P. ensifolia</i>	ovoid	smooth	absent	1.3-1.4 x 1.1-1.2	0.1	ridged
<i>P. longituba</i>	ovoid	smooth	absent	1.3-1.4 x 1.3-1.4	0.1	ridged
<i>P. maughanii</i>	ovoid	smooth	absent	1.3-1.4 x 1.3-1.4	0.1	ridged
<i>P. paucifolia</i>	globose	smooth	absent	1.1-1.2 x 1.3	0.1	ridged
<i>Massonia</i>	globose	smooth	absent	0.9-1.4 x 0.8-1.4	0.1-0.3	ridged

5) **Testa primary sculpturing.** Two states occurred: smooth (=0); and rugose (=1). Qualitative character, scored as character 67 (Appendix 1).

Primary testa sculpturing in *Massonia* as well as in 113 (94%) ingroup species (109 *Lachenalia*, four *Polyxena*), was smooth. In seven (6%) *Lachenalia* and *Polyxena* species seeds were rugose, *L. bolusii*, *L. buchbergensis*, *L. komsbergensis*, *L. patula*, *L. polyphylla*, *L. wiesei* and *P. corymbosa* (Figure 42 A-C, Table 42).

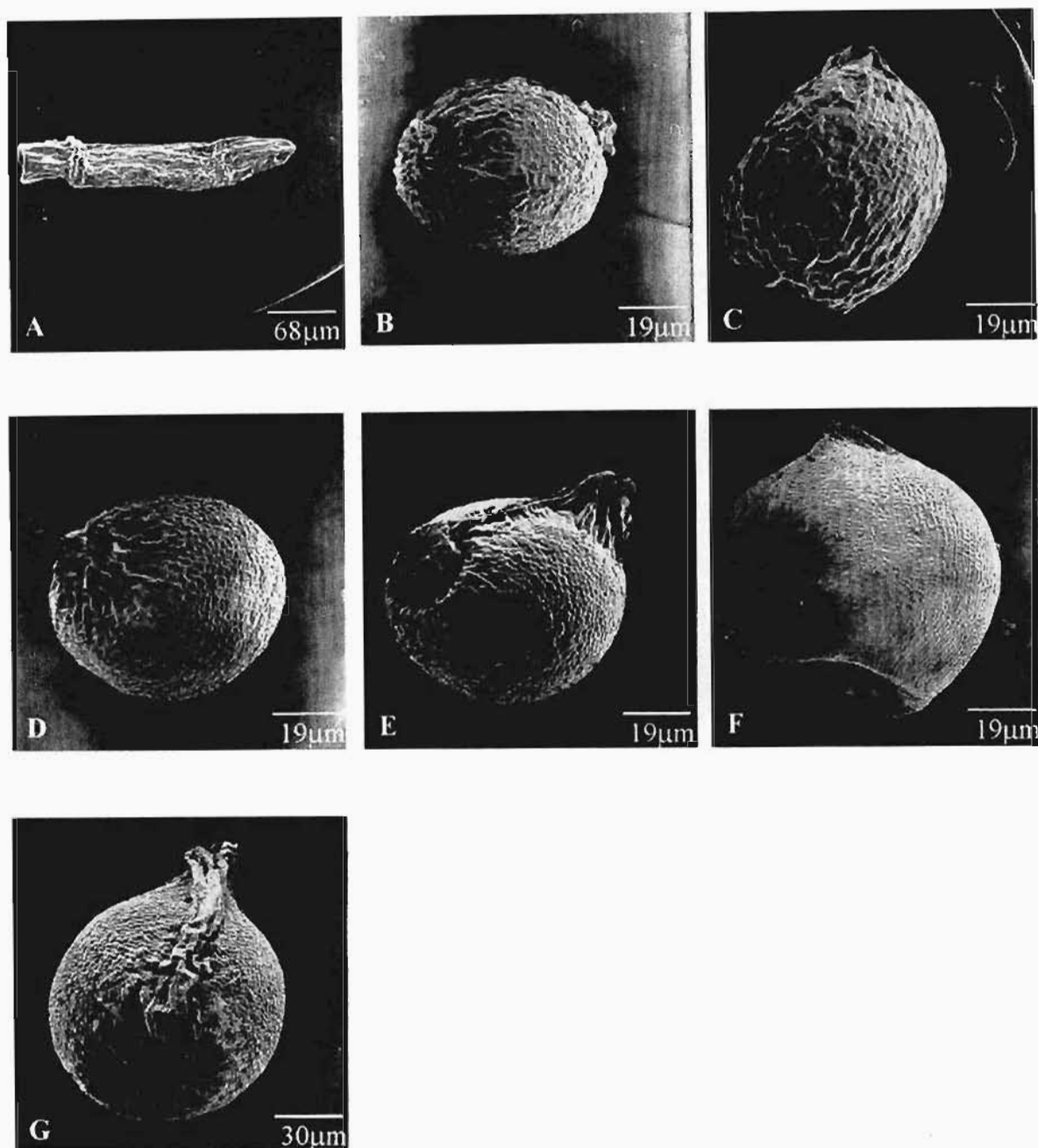


Figure 42. Scanning electron micrographs illustrating variation in primary and secondary sculpturing of the testa in *Lachenalia*.

Primary sculpturing: rugose testa of A, *L. buchbergensis* (Lavranos s.n.); B, *L. patula* (Jamieson 60); C, *L. polyphylla* (Duncan 348).

Secondary sculpturing: reticulate testa of D, *L. angelica* (Duncan 244); E, *L. framesii* (Duncan 99); F, *L. hirta* var. *hirta* (Duncan 77); colliculate testa of G, *L. montana* (Duncan 268).

6) **Testa secondary sculpturing.** Three states occurred: secondary sculpturing absent (=0); reticulate (=1); and colliculate (=2). Qualitative character, scored as character 68 (Appendix 1).

Secondary testa sculpturing was absent from *Massonia* and 106 (88%) ingroup species (101 *Lachenalia*, all five *Polyxena*). In 12 (10%) *Lachenalia* species secondary sculpturing was reticulate, *L. angelica*, *L. bowkeri*, *L. dehoopensis*, *L. framesii*, *L. glauca*, *L. hirta* (both varieties), *L. inconspicua*, *L. karooica*, *L. namaquensis*, *L. perryae*, *L. polypodantha* and *L. trichophylla* (both subspecies), and two (2%) *Lachenalia* species had colliculate secondary sculpturing, *L. montana* and *L. sargeantii* (Figure 42 D-G, Table 42).

7) **Strophiole length.** Three discontinuous states occurred: rudimentary strophioles (=0); medium strophioles (=1) and long strophioles (=2). Quantitative character, scored as character 69 (Appendix 1).

Massonia had rudimentary strophioles up to 0.3 mm long, as did 47 (39%) ingroup species (42 *Lachenalia*, all five *Polyxena*) (Figure 43A-D). Sixty (50%) *Lachenalia* species had medium strophioles 0.5-0.8 mm long, and 13 (11%) *Lachenalia* species had long strophioles 1.1 mm long or longer (Figures 43E-H, 44, Table 42). *L. aloides* var. *vanzyliae* and *L. bulbifera* had the longest strophioles (respectively 1.4-1.5 mm and 1.4-1.6 mm long).

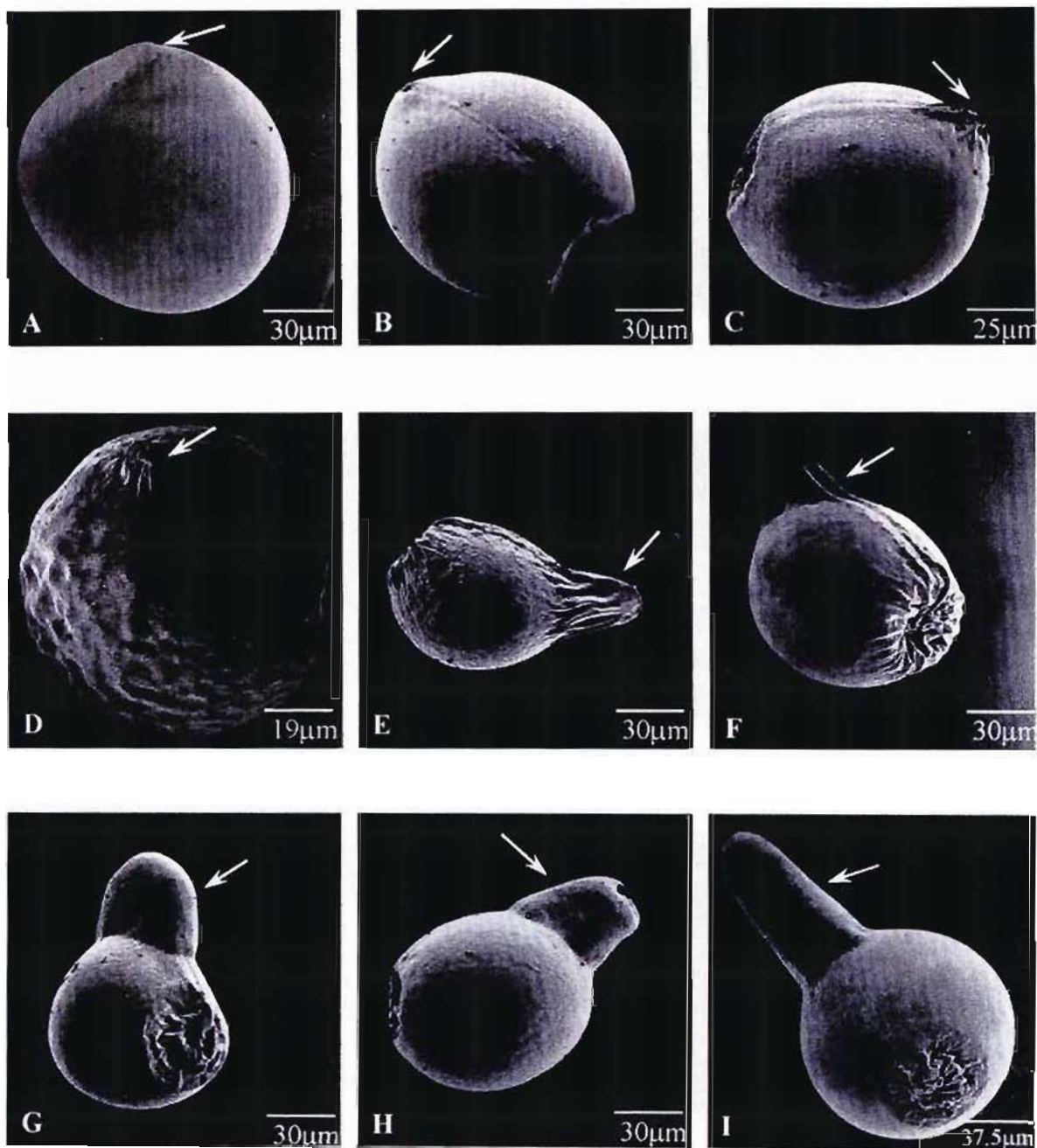


Figure 43. Scanning electron micrographs illustrating variation in strophiole length in *Lachenalia* and *Polyxena*. Rudimentary strophioles of A, *L. isopetala* (Perry 3065); B, *L. namibiensis* (Lavranos 19955); C, *L. pustulata* (Duncan 411); D, *P. paucifolia* (Duncan 170). Medium-length strophioles of E, *L. dasybotrya* (Thomas 8); F, *L. latimerae* (Vorster 3028); G, *L. ventricosa* (Duncan 285); H, *L. viridiflora* (Duncan 410). Long strophiole of I, *L. aloides* var. *vanzyliae* (Thomas s.n.).

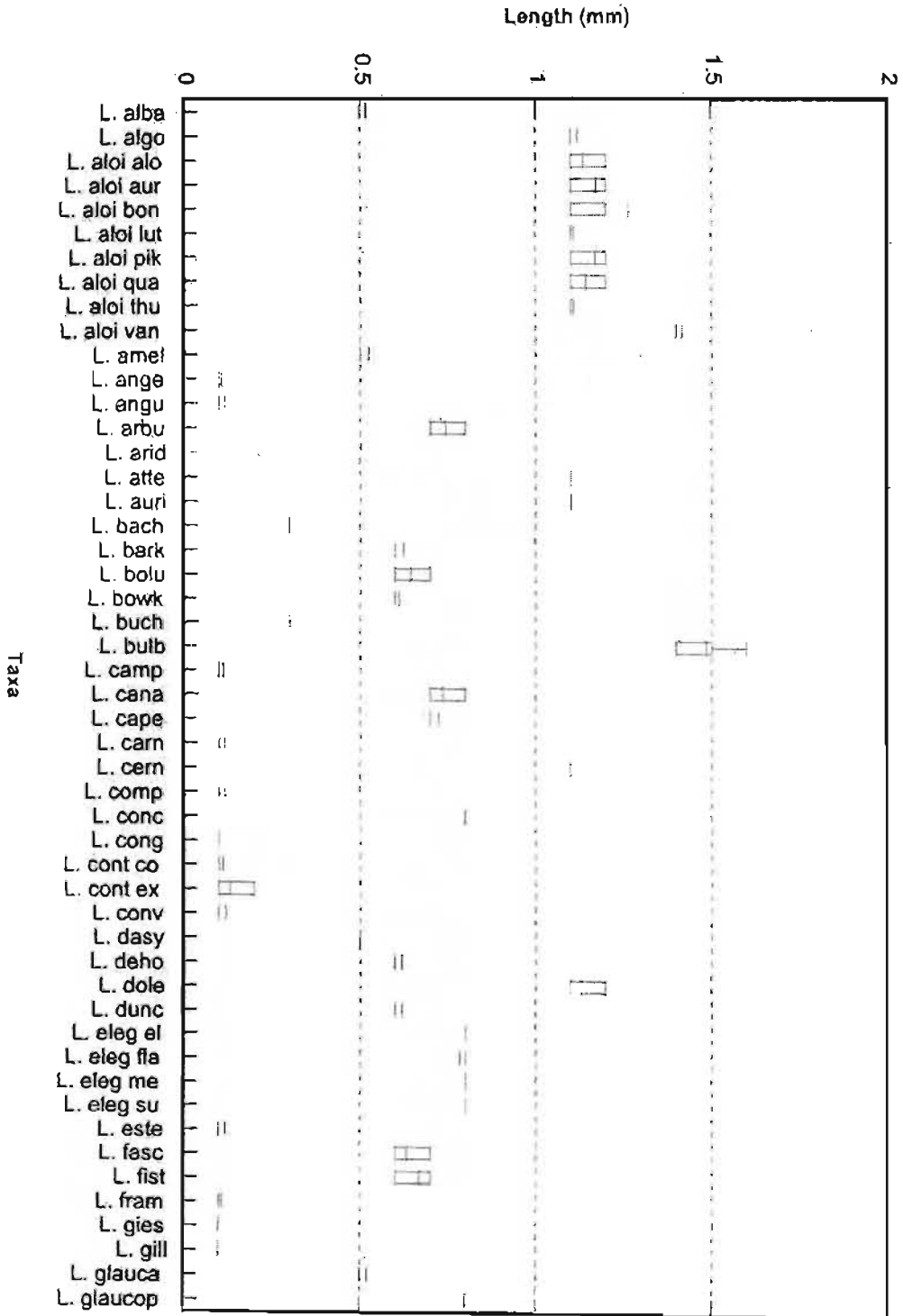


Figure 44. Strophiole length in Lachenalia and Polyxena

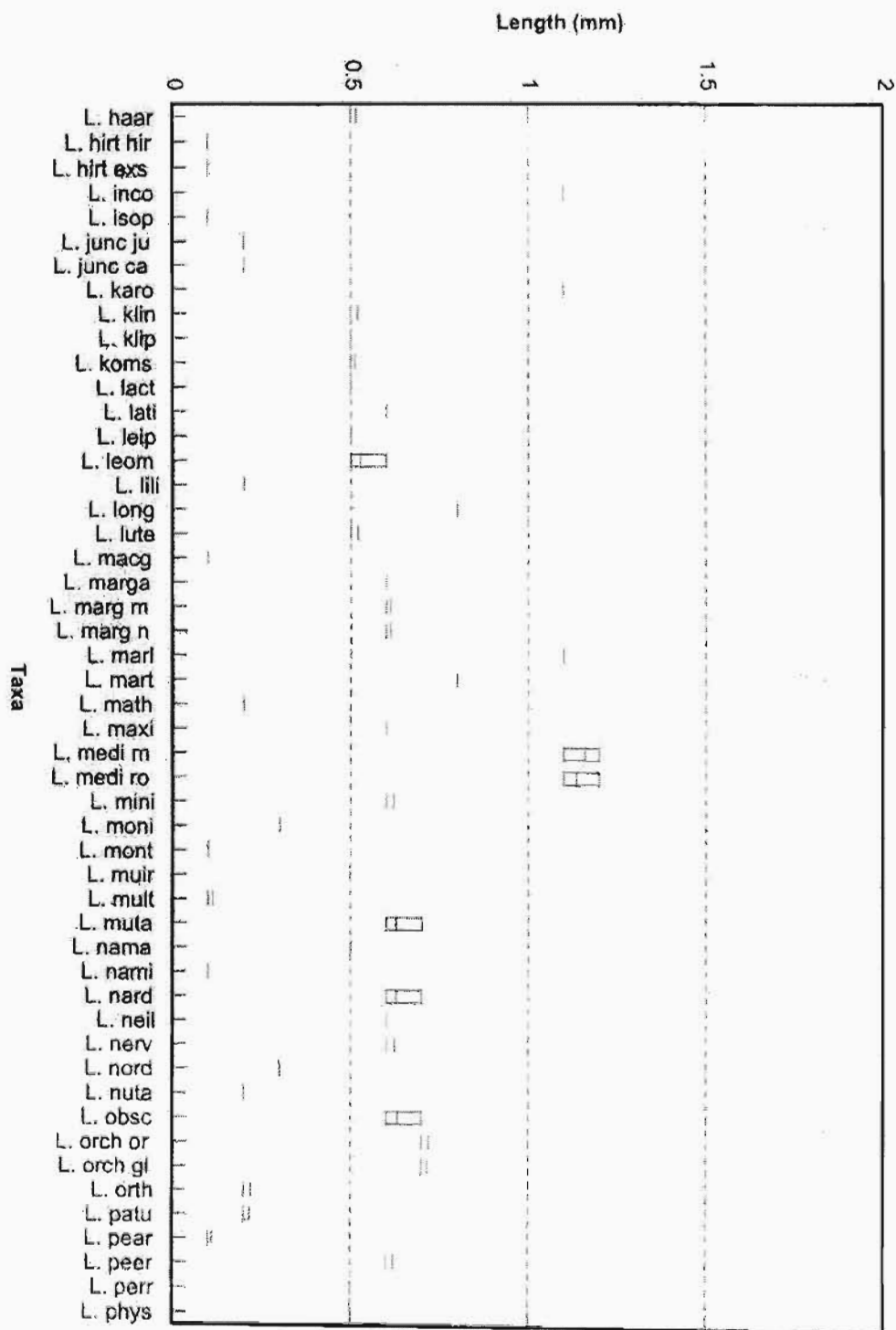


Figure 44. Strophiole length in Lichenalia and Polyxena

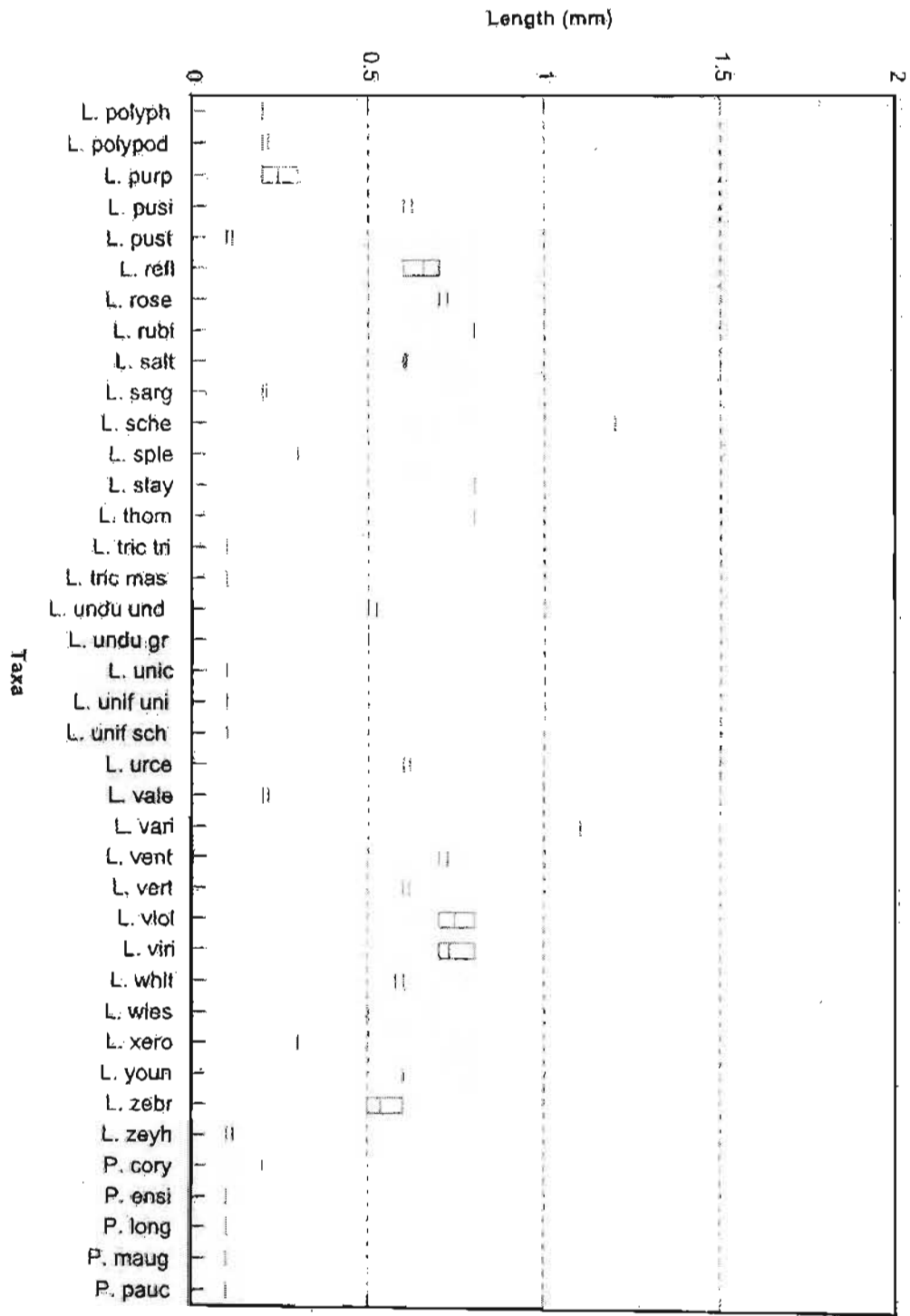


Figure 44. Strophiole length in Lachenaillia and Polyxena

8) **Strophiole texture.** Two states occurred: ridged strophioles (=0); and smooth strophioles (=1). Qualitative character, scored as character 70 (Appendix 1).

Ridged strophioles occurred in *Massonia*, as well as in 81 (67.5%) ingroup species (76 *Lachenalia*, all five *Polyxena*) (Figure 43A-F). In 39 (32.5%) *Lachenalia* species, strophioles were smooth (Figure 43G-I, Table 42).

9) **Strophiole inflation.** Two states occurred: non-inflated strophioles (=0); and inflated strophioles (=1). Qualitative character, scored as character 71 (Appendix 1).

Massonia and 81 (67.5%) ingroup species (76 *Lachenalia*, all five *Polyxena*) had non-inflated strophioles (Figure 43A-F). In 39 (32.5%) *Lachenalia* species, the strophioles were distinctly inflated (Figure 43G-I, Table 43). The inflated strophiole of *L. bulbifera* was noteworthy in being translucent white. In *L. barkeriana* and *L. pusilla*, epidermal cells were fairly prominent on the surfaces of their inflated strophioles.

Character State	Species
Non-inflated	<i>L. alba</i> , <i>L. ameliae</i> , <i>L. angelica</i> , <i>L. anguinea</i> , <i>L. arida</i> , <i>L. attenuata</i> , <i>L. aurioliae</i> , <i>L. bachmannii</i> , <i>L. bowkeri</i> , <i>L. buchbergensis</i> , <i>L. campanulata</i> , <i>L. canaliculata</i> , <i>L. carnosa</i> , <i>L. comptonii</i> , <i>L. concordiana</i> , <i>L. congesta</i> , <i>L. contaminata</i> (both varieties), <i>L. convallarioides</i> , <i>L. dasybotrya</i> , <i>L. dehoopensis</i> , <i>L. doleritica</i> , <i>L. duncanii</i> , <i>L. esterhuysenae</i> , <i>L. fasciculata</i> , <i>L. framesii</i> , <i>L. giessii</i> , <i>L. gillettii</i> , <i>L. glaucophylla</i> , <i>L. haarlemensis</i> , <i>L. hirta</i> (both varieties), <i>L. inconspicua</i> , <i>L. isopetala</i> , <i>L. juncifolia</i> (both varieties), <i>L. karooica</i> , <i>L. klinghardtiana</i> , <i>L. kliprandensis</i> , <i>L. komsbergensis</i> , <i>L. latimerae</i> , <i>L. liliiflora</i> , <i>L. macgregoriorum</i> , <i>L. mathewsii</i> , <i>L. maximiliani</i> , <i>L. minima</i> , <i>L. moniliformis</i> , <i>L. montana</i> , <i>L. multifolia</i> , <i>L. namaquensis</i> , <i>L. namibiensis</i> , <i>L. nardouwensis</i> , <i>L. neilii</i> , <i>L. nordenstamii</i> , <i>L. nutans</i> , <i>L. obscura</i> , <i>L. orthopetala</i> , <i>L. patula</i> , <i>L. pearsonii</i> , <i>L. perryae</i> , <i>L. polyphylla</i> , <i>L. polypodantha</i> , <i>L. purpureocaerulea</i> , <i>L. pustulata</i> , <i>L. sargeantii</i> , <i>L. schelpei</i> , <i>L. splendida</i> , <i>L. trichophylla</i> (both subspecies), <i>L. undulata</i> (both subspecies), <i>L. unicolor</i> , <i>L. unifolia</i> (both varieties), <i>L. urceolata</i> , <i>L. valeriae</i> , <i>L. verticillata</i> , <i>L. whitehillensis</i> , <i>L. wiesei</i> , <i>L. xerophila</i> , <i>L. zebrina</i> , <i>L. zeyheri</i> <i>P. corymbosa</i> , <i>P. ensifolia</i> , <i>P. longituba</i> , <i>P. maughanii</i> , <i>P. paucifolia</i> <i>Massonia</i>
Inflated	<i>L. algoensis</i> , <i>L. aloides</i> (all eight varieties), <i>L. arbutnotiae</i> , <i>L. barkeriana</i> , <i>L. bolusii</i> , <i>L. bulbifera</i> , <i>L. capensis</i> , <i>L. cermua</i> , <i>L. elegans</i> (all four varieties), <i>L. fistulosa</i> , <i>L. glauca</i> , <i>L. lactosa</i> , <i>L. leipoldtii</i> , <i>L. leomontana</i> , <i>L. longibracteata</i> , <i>L. lutea</i> , <i>L. margaretae</i> , <i>L. marginata</i> (both subspecies), <i>L. marlothii</i> , <i>L. martinae</i> , <i>L. mediana</i> (both varieties), <i>L. muirii</i> , <i>L. mutabilis</i> , <i>L. nervosa</i> , <i>L. orchioides</i> (both varieties), <i>L. peersii</i> , <i>L. physocaulos</i> , <i>L. pusilla</i> , <i>L. reflexa</i> , <i>L. rosea</i> , <i>L. rubida</i> , <i>L. salteri</i> , <i>L. stayneri</i> , <i>L. thomasiae</i> , <i>L. variegata</i> , <i>L. ventricosa</i> , <i>L. violacea</i> , <i>L. viridiflora</i> , <i>L. youngii</i>

10) **Raphe inflation.** Two states occurred: non-inflated raphes (=0); and inflated raphes (=1). Qualitative character, scored as character 72 (Appendix 1).

The raphe is the longitudinal ridge which forms below the hilum (Figure 38). *Massonia* and 117 (97.5%) ingroup species (112 *Lachenalia*, all five *Polyxena*) had non-inflated raphes. In three (2.5%) *Lachenalia* species (*L. bulbifera*, *L. rubida* and *L. xerophila*), the raphe was distinctly inflated, and it joined with the inflated strophiole. The micropyle was situated very close to the hilum (Figure 38), on page 170.

11) **Chalazal collar length.** Three states occurred: collars absent (=0), short collars (=1) and long collars (=2). Quantitative character, scored as character 73 (Appendix 1).

Collars were absent in *Massonia* and 94 (78%) ingroup species (89 *Lachenalia*, all five *Polyxena*) (Figure 43B, C, E, F, H). Twenty-four (20%) *Lachenalia* species had short collars up to 0.4 mm long (Figure 43G), and in two (2%) *Lachenalia* species the collars were long (0.8 mm long or longer) (Figures 42A, 45, Table 44).

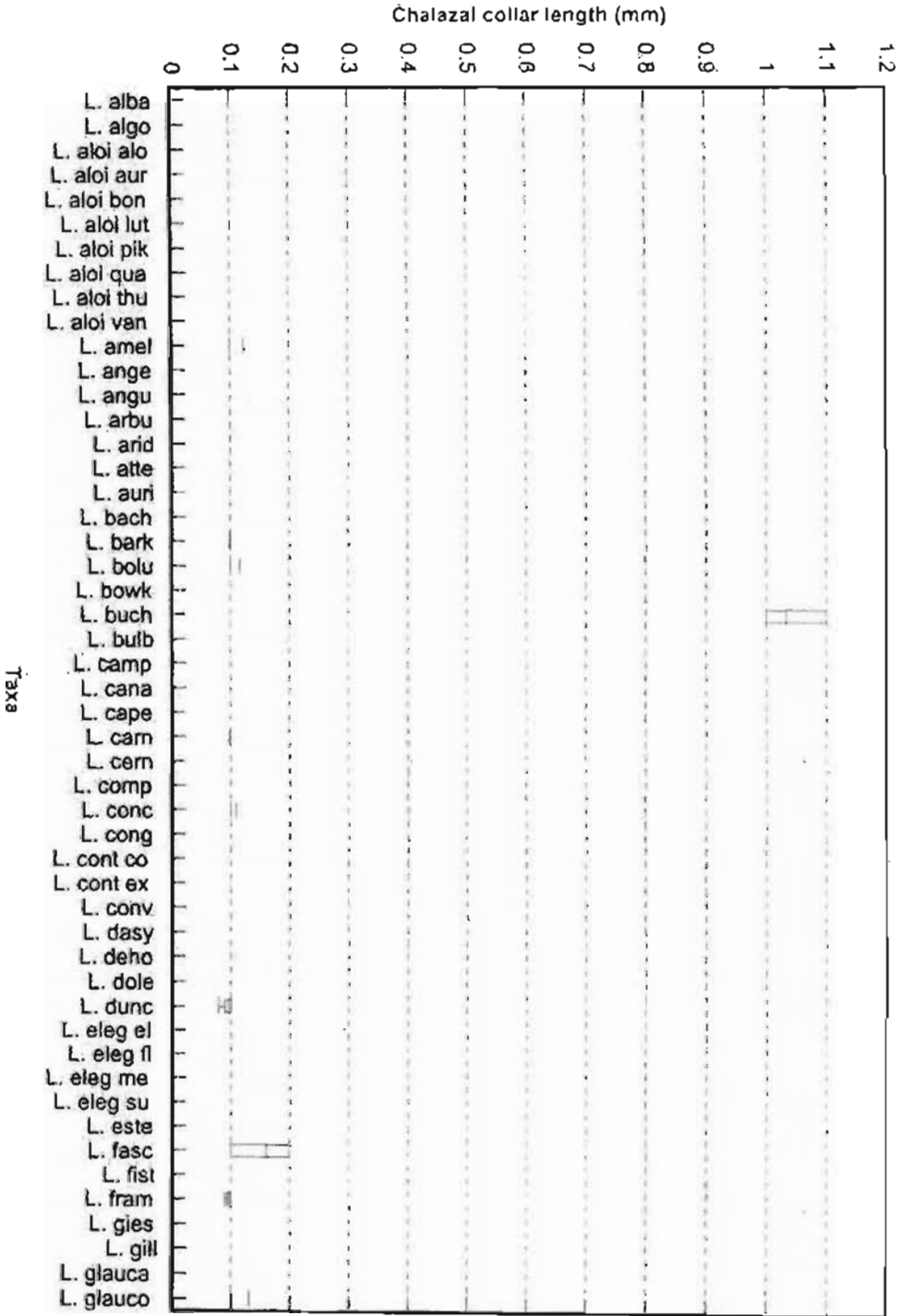


Figure 45. Chalazal collar length in Lachenalia and Polyxena

Figure 45. Chalazal collar length in *Lachenalia* and *Polyxena*



Figure 45. Chalazal collar length in Lachenalia and Polyxena

Table 44. Variation in chalazal collar length in *Lachenalia*, *Polyxena* and the outgroup *Massonia*

Character state	Species
Absent	<i>L. alba</i> , <i>L. algoensis</i> , <i>L. aloides</i> (all eight varieties), <i>L. angelica</i> , <i>L. anguinea</i> , <i>L. arbutnotiae</i> , <i>L. arida</i> , <i>L. attenuata</i> , <i>L. auriolae</i> , <i>L. bachmannii</i> , <i>L. bowkeri</i> , <i>L. bulbifera</i> , <i>L. campanulata</i> , <i>L. canaliculata</i> , <i>L. capensis</i> , <i>L. cernua</i> , <i>L. comptonii</i> , <i>L. congesta</i> , <i>L. contaminata</i> (both varieties), <i>L. convallarioides</i> , <i>L. dasybotrya</i> , <i>L. dehoopensis</i> , <i>L. doleritica</i> , <i>L. elegans</i> (all four varieties), <i>L. esterhuysenae</i> , <i>L. fistulosa</i> , <i>L. giessii</i> , <i>L. gillettii</i> , <i>L. glauca</i> , <i>L. haarlemensis</i> , <i>L. hirta</i> (both varieties), <i>L. inconspicua</i> , <i>L. isopetala</i> , <i>L. juncifolia</i> (both varieties), <i>L. karoocica</i> , <i>L. kliprandensis</i> , <i>L. komsbergensis</i> , <i>L. lactosa</i> , <i>L. latimerae</i> , <i>L. leipoldtii</i> , <i>L. leomontana</i> , <i>L. liliiflora</i> , <i>L. longibracteata</i> , <i>L. lutea</i> , <i>L. macgregoriorum</i> , <i>L. margaretae</i> , <i>L. marginata</i> (both subspecies), <i>L. mathewsii</i> , <i>L. maximiliani</i> , <i>L. mediana</i> (both varieties), <i>L. moniliformis</i> , <i>L. martinae</i> , <i>L. montana</i> , <i>L. muirii</i> , <i>L. multifolia</i> , <i>L. namaquensis</i> , <i>L. namibiensis</i> , <i>L. nardouwensis</i> , <i>L. neilii</i> , <i>L. nervosa</i> , <i>L. mutans</i> , <i>L. obscura</i> , <i>L. orchioides</i> (both varieties), <i>L. orthopetala</i> , <i>L. pearsonii</i> , <i>L. peersii</i> , <i>L. physocaulos</i> , <i>L. polyphylla</i> , <i>L. polypodantha</i> , <i>L. purpureocaerulea</i> , <i>L. pustulata</i> , <i>L. reflexa</i> , <i>L. rosea</i> , <i>L. salteri</i> , <i>L. sargeantii</i> , <i>L. schelpei</i> , <i>L. splendida</i> , <i>L. stayneri</i> , <i>L. thomasiae</i> , <i>L. unicolor</i> , <i>L. unifolia</i> (both varieties), <i>L. urceolata</i> , <i>L. variegata</i> , <i>L. violacea</i> , <i>L. viridiflora</i> , <i>L. whitehillensis</i> , <i>L. wiesei</i> , <i>L. youngii</i> , <i>L. zeyheri</i> <i>P. corymbosa</i> , <i>P. ensifolia</i> , <i>P. longituba</i> , <i>P. maughanii</i> , <i>P. paucifolia</i> <i>Massonia</i>
Short	<i>L. ameliae</i> , <i>L. barkeriana</i> , <i>L. bolusii</i> , <i>L. carnosa</i> , <i>L. concordiana</i> , <i>L. duncanii</i> , <i>L. fasciculata</i> , <i>L. framesii</i> , <i>L. glaucophylla</i> , <i>L. klinghardtiana</i> , <i>L. marlothii</i> , <i>L. minima</i> , <i>L. mutabilis</i> , <i>L. patula</i> , <i>L. perryae</i> , <i>L. pusilla</i> , <i>L. rubida</i> , <i>L. trichophylla</i> (both subspecies), <i>L. undulata</i> (both subspecies), <i>L. valeriae</i> , <i>L. ventricosa</i> , <i>L. verticillata</i> , <i>L. xerophila</i> , <i>L. zebrina</i>
Long	<i>L. buchubergensis</i> , <i>L. nordenstamii</i>

5.20 KARYOLOGY

The karyology of *Lachenalia* is extremely variable, including different basic chromosome numbers, as well as different ploidy levels and B-chromosomes (extra chromosomes) within some species.

Chromosome counts are available for 55 *Lachenalia* species (Moffett 1936, de Wet 1957, Riley 1962, Ornduff & Watters 1978, Nordenstam 1982, Crosby 1986, Hancke & Liebenberg 1990, Hancke 1991, Duncan 1993, Duncan 1996, Johnson & Brandham 1997, Hamatani *et al.* 1998, Kleynhans & Spies 1999, Spies *et al.* 2000, Spies *et al.* 2002, van Rooyen *et al.* 2002) (Table 45). The basic chromosome numbers $x = 5, 6, 7, 8, 9, 10, 11, 13$ and 15 have been recorded, with $x = 7$ and $x = 8$ being the most frequent. Ploidy levels are

predominantly diploid, but tetraploid, hexaploid and octoploid counts have been made. Intraspecific polyploidy has been reported in several 'species'. Diploids and tetraploids occur in *L. orchioides*, tetraploids and octoploids occur in *L. elegans* (Ornduff & Watters 1978), and *L. bulbifera* forms a polyploid complex (Kleynhans & Spies 1999). According to Spies *et al.* (2002), polyploidy is quite common in *Lachenalia*, and is present in 24 (44%) species studied so far. They caution that the high level of 'deviating' counts (recorded for 16 species) may be due to the misidentification of B-chromosomes and the incorrect identification of specimens studied. They also postulate that the different basic chromosome numbers for *Lachenalia* indicate that aneuploidy (having a diploid chromosome number that is not an exact multiple of the haploid number because one chromosome set is incomplete or fused) played a major role in the evolution of the genus, but that it is doubtful that as many as 16 species could contain aneuploid representatives.

Table 45. Variation in chromosome number in *Lachenalia*

Species	Chromosome number (2n)	Authority and year of publication
<i>L. alba</i>	18, 20, 40	Johnson & Brandham (1997)
<i>L. algoensis</i>	14	Crosby (1986)
<i>L. aloides</i>	14 28	Crosby (1986), Johnson & Brandham (1997), Hamatani (1998)
<i>L. ameliae</i>	18	Johnson & Brandham (1997)
<i>L. anguinea</i>	30 +2B	Johnson & Brandham (1997)
<i>L. arbutnotiae</i>	14	Crosby (1986), Johnson & Brandham (1997)
<i>L. bachmannii</i>	16	De Wet (1957), Crosby (1986), Hancke (1991), Johnson & Brandham (1997)
<i>L. barkeriana</i>	14, 16 16	Müller-Doblies <i>et al.</i> (1987), Nordenstam (1982)
<i>L. bulbifera</i>	14, 56 28, 42 28, 42, 49, 56	Crosby (1986), Moffett (1936), Kleynhans & Spies (1999)
<i>L. capensis</i>	c28	Johnson & Brandham (1997)
<i>L. carnosa</i>	16	Johnson & Brandham (1997), Hamatani (1998)
<i>L. comptonii</i>	20	Crosby (1986), Johnson & Brandham (1997)
<i>L. congesta</i>	26,28	Johnson & Brandham (1997)
<i>L. contaminata</i>	16, 16 +1B, 32	Johnson & Brandham (1997)
<i>L. convallarioides</i>	30	Johnson & Brandham (1997)
<i>L. elegans</i>	14, 28, 42	Johnson & Brandham (1997)
<i>L. fistulosa</i>	14	Ornduff & Watters (1978), Johnson & Brandham (1997)
<i>L. haarlemensis</i>	18	Johnson & Brandham (1997)
<i>L. hirta</i>	22, 24 22	Johnson & Brandham (1997), Van Rooyen <i>et al.</i> (2002)
<i>L. isopetala</i>	30	Johnson & Brandham (1997)
<i>L. juncifolia</i>	22	Johnson & Brandham (1997), Spies <i>et al.</i> (2002)
<i>L. karooica</i>	16	Duncan (1996)
<i>L. kliprandensis</i>	16	Johnson & Brandham (1997)
<i>L. nervosa</i>	24	Johnson & Brandham (1997)
<i>L. liliiflora</i>	16	De Wet (1957), Hancke (1991), Johnson & Brandham (1997), Hamatani (1998)
<i>L. longibracteata</i>	14	Crosby (1986)
<i>L. marginata</i>	28, 29	Johnson & Brandham (1997)
<i>L. mathewsii</i>	14	Johnson & Brandham (1997), Spies <i>et al.</i> (2002)
<i>L. mediana</i>	14 26	Johnson & Brandham (1997), Crosby (1986), Spies <i>et al.</i> (2002)
<i>L. muirii</i>	14	Johnson & Brandham (1997)

Table 45. Variation in chromosome number in *Lachenalia*

Species	Chromosome number (2n)	Authority and year of publication
<i>L. mutabilis</i>	10, 14 12, 14, 24 14, 56	Johnson & Brandham (1997), Spies <i>et al.</i> (2000), De Wet (1957)
<i>L. namaquensis</i>	16	Crosby (1986), Johnson & Brandham (1997)
<i>L. obscura</i>	18, 18 + 1B	Johnson & Brandham (1997)
<i>L. orchioides</i>	16 16, 17 28, 29	De Wet (1957), Moffett (1936), Johnson & Brandham (1997)
<i>L. orthopetala</i>	16	Crosby (1986), Johnson & Brandham (1997)
<i>L. peersii</i>	14	Johnson & Brandham (1997)
<i>L. purpureocaerulea</i>	16	Ornduff & Watters (1978), Johnson & Brandham (1997)
<i>L. pusilla</i>	14	Crosby (1986), Johnson & Brandham (1997)
<i>L. pustulata</i>	16	Crosby (1986), Johnson & Brandham (1997), Spies <i>et al.</i> (2000)
<i>L. reflexa</i>	14	Crosby (1986), Johnson & Brandham (1997)
<i>L. rosea</i>	14 14, 21	Johnson & Brandham (1997) Crosby (1986)
<i>L. rubida</i>	14, 28	Crosby (1986)
<i>L. splendida</i>	16	Crosby (1986), Johnson & Brandham (1997)
<i>L. stayneri</i>	24	Johnson & Brandham (1997)
<i>L. thomasiae</i>	14	Duncan (1993)
<i>L. trichophylla</i>	14	Ornduff & Watters (1978), Johnson & Brandham (1997)
<i>L. undulata</i>	20	Johnson & Brandham (1997)
<i>L. unicolor</i>	16 16, 32	Johnson & Brandham (1997), Spies <i>et al.</i> (2000), Crosby (1986)
<i>L. unifolia</i>	22 22, 44	Crosby (1986), Van Rooyen <i>et al.</i> (2002), Johnson & Brandham (1997)
<i>L. variegata</i>	28	Spies <i>et al.</i> (2002)
<i>L. verticillata</i>	16	Crosby (1986)
<i>L. violacea</i>	14 14, 15 14, 16	Ornduff & Watters (1978), Hamatani <i>et al.</i> (1998), Johnson & Brandham (1997), Crosby (1986)
<i>L. viridiflora</i>	14	Nordenstam (1982), Crosby (1986), Johnson & Brandham (1997), Spies <i>et al.</i> (2002)
<i>L. zebrina</i>	30	Johnson & Brandham (1997)
<i>L. zeyheri</i>	22	Johnson & Brandham (1997)

L. mutabilis may represent an aneuploid series (Spies *et al.* 2000) but is currently regarded as a single morphologically variable species complex. Different basic chromosome numbers, $x = 5$, $x = 6$ and $x = 7$ have been reported by various authors. Ornduff & Watters (1978) reported $x = 5$ for one collection, Johnson and Brandham (1997) reported $2n = 10$ for six collections and $2n = 14$ for two collections, and Spies *et al.* (2000) reported $x = 6$ and $x = 7$ for 35 specimens representing 16 populations. Robertsonian fusions have been shown to be important in the chromosomal evolution of other plant families, e.g. the Commelinaceae (Jones 1976). Johnson & Brandham (1997) suggested that the different chromosome numbers in *L. mutabilis* could be attributed to Robertsonian translocations, which result in dysploidy. They postulated that plants with $x = 5$ are derived from plants with $2n = 14$ via two Robertsonian fusions. They recorded one such fusion between two acrocentric chromosomes at the centromere to produce a single larger chromosome, with the associated loss of the short arms, thus lowering the chromosome number by one. A homozygote for the fusion would have two chromosomes fewer than the normal number, and a homozygote for two independent fusions would have four fewer (Johnson & Brandham 1997). Variation in chromosome morphology occurs between different wild localities, and even between specimens from the same locality (Spies *et al.* 2000), although most specimens of *L. mutabilis* have four to eight very short chromosomes. The number of short chromosomes varies between different localities and between specimens collected at the same locality, and no evidence of longer chromosomes (as a result of Robertsonian translocations) was found in any of the specimens studied, therefore the Robertsonian translocation hypothesis has been discounted by them (Spies *et al.* 2000). These authors have postulated that an aneuploid series may exist in *L. mutabilis*, and found that different specimens collected within the same population showed no variation in chromosome number, but vary geographically from one population to another. To test this hypothesis, thorough meiotic studies, including cross fertilizations between *L. mutabilis* specimens will need to be completed. The difference in basic chromosome number for this species is not correlated to geographical position, as certain populations occurring relatively close to each other have different basic chromosome numbers. Spies *et al.* (2000), reported that polyploidy is scarce in *L. mutabilis*; as a result of a cytogenetic study of 35 specimens

representing 16 populations, only 5 % of specimens exhibited this phenomenon.

While polymorphism of peduncle inflation is acceptable at the species level, speciation is almost certainly taking place in the *L. mutabilis* complex since morphological divergence is being entrenched by breeding barriers at the chromosome level.

The robust, widespread species *L. bulbifera* is an example of a polyploid complex within the genus, and has a basic chromosome number of $x = 7$, with ploidy levels ranging from diploid to octoploid, with chromosome numbers of $2n = 14, 28, 42, 49$ and 56 (Kleynhans & Spies 1999). Ploidy levels for this species are the same for all individuals within populations. The differences in ploidy level are probably the product of founder effect, where, for example, octoploid populations identified by Kleynhans & Spies (1999) in the southern Cape, are probably derived from cross fertilizations between tetraploid founder populations in this area. The *L. bulbifera* complex has undergone chromosomal divergence generating a number of species, but morphological evolution in this complex is still in progress and differentiation into distinct morphospecies is difficult. Morphological variation in *L. bulbifera* is thus better correlated with geographical distribution than with ploidy level (Kleynhans & Spies 1999).

In a further study of genetic variation in *L. bulbifera*, Kleynhans & Spies (2000) tested the feasibility of detecting intra-specific variation in this species using randomly amplified polymorphic DNA (RAPD). The genetic distance values obtained from 21 accessions of this species complex revealed a high level of variation, and showed that different hexaploid and tetraploid accessions were grouped together in different RAPD clusters, inferring that accessions with the same chromosome number are not necessarily closely related.

Speciation as a result of ploidy changes occurs when gene flow is disrupted due to chromosomal incompatibility, as occurs in polyploidy and aneuploidy. Here the species may occur sympatrically but do not share gene pools. The differentiation of numerous morphological and cytological forms in species like *L. bulbifera* and *L. mutabilis* appear to

point to a state of rapid evolution among certain groups.

Johnson and Brandham (1997) report that all the basic chromosome numbers $x = 7-13$ and 15 produce structural diploids with twice the number, (i.e. a number of $2n = 20$ represents a diploid based on $x = 10$ rather than a tetraploid based on $x = 5$). It was speculated that diploids with $2n = 30$ ($x = 15$) could actually be allotetraploids derived from taxa with $x = 7$ and $x = 8$, following hybridisation and doubling of the chromosome number.

B-chromosomes (extra chromosomes) have been reported for sixteen species in *Lachenalia* (Spies *et al.* 2002). They differ morphologically from the chromosomes of the normal complement in being smaller and are heterochromatic, but these characteristics are variable (Jones & Rees 1982). In a cytogenetic study, Hancke & Liebenberg (1990) found B-chromosomes in somatic and meiotic material of some species and in F1 hybrids. In addition to the normal complement, one to three B-chromosomes were observed in some of the cells of several species as well as in F1 hybrids, and were similar in size to the smallest chromosome of the normal complement. This irregular occurrence of B-chromosomes accounts for variation in chromosome counts between vegetatively similar plants of some species, such as *L. orchioides*, by different researchers (de Wet 1957; Moffett 1936; Riley 1962; Johnson & Brandham 1997).

Differences in basic chromosome number of *Lachenalia* results in breeding barriers between sympatric species where the flowering periods overlap. This explains the exceptionally low incidence of natural hybrids between some species. As an example, in a large population of *L. mathewsii* ($x = 7$) and *L. pustulata* ($x = 8$) growing sympatrically near Vredenburg on the Cape west coast, the flowering time in mid-September overlaps for a period of at least two weeks, yet no natural hybrids have ever been observed there over a ten-year period despite intense pollination activity by honey-bees visiting both species. Similarly, no natural hybrids have been seen between *L. contaminata* ($x = 8$) and *L. polyphylla* ($x =$ unknown) growing sympatrically near Gouda in the southwestern Cape where the flowering

time in mid-September overlaps for about two weeks in mid-September, where both species are visited by honey-bees. The only known record of a natural hybrid in *Lachenalia* is between two taxa currently recognised as varieties under *L. aloides*, both of which occur on the Piketberg Mountains in the Western Cape, i.e. the very unusually-coloured turquoise and green flowers of *L. aloides* var. *vanzyliae*, and the bright orangey-yellow flowers of *L. aloides* var. *piketbergensis* (W.F. Barker manuscript name). In this instance the single individual was clearly a hybrid between the two taxa as it had flowers of intermediate colour and length (Barker 1984). The hybrid individual clearly indicated F1 expression, being intermediate between the two taxa, indicating that breeding barriers between the two taxa must be maintaining species identity. As no hybrid swarms occur between the two taxa (that occur in close proximity), and both taxa almost certainly having the same sunbird pollinator, recognition of both taxa as separate species is warranted.

6 INFRAGENERIC CLASSIFICATION

6.1 SPECIES CONCEPTS

Species concepts have fluctuated tremendously over the past two and a half centuries, ranging from broad species concepts (artificial classifications) of the eighteenth century (Linnaeus 1771, 1784), to narrow species concepts (taxonomic species) of the nineteenth and early twentieth centuries (Baker 1871, 1897), the latter were the result of narrow disciplinary approaches, using mainly macromorphological characters. The modern multidisciplinary approach of macro- and micromorphology, cytogenetics, molecular, palynological, anatomical, and phytogeographical research has generally had a stabilizing effect on species concepts (Cronquist 1981).

The species concept applied in this thesis is a combination of the morpho-species and the biological species concepts, adapted from the phylogenetic species concept of Nixon and Wheeler (1990), defined as the smallest aggregation of freely interbreeding populations or lineages reproductively isolated from other such populations, diagnosable by a unique combination of character states in comparable individuals.

Morphological characters vary in importance in delimiting a species. Relatively uninformative characters like leaf and bulb size, and overall plant size can vary tremendously depending on environmental conditions. In *Lachenalia* and *Polyxena*, stable characters such as bulb, leaf and perianth shape, filament orientation, capsule and seed shape, and strophiole length are not greatly affected by environmental conditions, and are therefore of much greater value in setting species limits. The extremely low incidence of natural hybrids in *Lachenalia* is an indication of the importance of breeding barriers resulting from differences in chromosome number, pollinators and habitat preference. Phenological, ecological and geographic differences are also regarded as providing useful features in circumscribing species. Cryptic species such as

those which currently exist within the *L. bulbifera* and *L. mutabilis* complexes are at a point of divergence beyond which they will gradually attain distinction through genetic drift.

6.2 PHENOTYPIC AND GENOTYPIC VARIATION

The phenotype is the outward expression of characteristics conferred on an individual by its genotype. The extent to which a particular genotype can give rise to different phenotypes is referred to as phenotypic plasticity. The genus *Lachenalia* is phenotypically and genotypically diverse. Minor variations in microhabitat of many *Lachenalia* taxa often results in considerable phenotypic variation, such as in plant height, leaf size, leaf maculation, flower number and pedicel length. However, certain characters are under tight genetic control in *Lachenalia*. Cultivated plants often retain characters (such as leaf maculation and pustule density) which were previously thought to be plastic. Field studies in conjunction with cultivation records provide a better understanding of phenotypic plasticity. In order to distinguish genotypic from phenotypic variation, wild collections were studied under uniform growing conditions at Kirstenbosch Botanic Garden, over a period of six years, during which phenotypically stable and plastic characters were recorded (Table 46).

Table 46. Phenotypically stable and plastic characters in <i>Lachenalia</i> and <i>Polyxena</i>	
Stable Characters	Plastic Characters
Bulb shape	Leaf orientation
Bulb tissue colour	Leaf margin shape
Bulbil production	Primary seedling leaf orientation
Offset production	Peduncle elevation at anthesis
Bulb outer tunic texture	Peduncle inflation
Bulb apex outer tunics	
Inner cataphyll apex shape	
Inner cataphyll adhesion to clasping leaf bases	
Concrescent/non-concrescent leaf bases	
Leaf base markings	
Leaf number	
Pustulate/non-pustulate adaxial leaf surface	
Adaxial leaf trichomes	
Adaxial leaf maculation	
Leaf shape	
Distal lamina profile	
Basal lamina profile	
Leaf margin anatomy	
Leaf margin vesture	
Leaf apex shape	
Primary seedling leaf shape	
Rachis apical pigmentation	
Rachis apex structural white	
Lower bract shape	
Upper bract shape	
Inflorescence type	
Pedicel orientation at anthesis	
Perianth shape (tepal orientation)	
Perianth tube length	
Perianth tube shape	
Flower arrangement	
Outer tepal shape	
Outer tepal length	
Outer tepal apex shape	
Inner tepal shape	
Inner tepal length	

Table 46. Phenotypically stable and plastic characters in <i>Lachenalia</i> and <i>Polyxena</i>	
Stable Characters	Plastic Characters
Inner and outer tepal arrangement	
Floral symmetry	
Ventral inner tepal extension	
Filament orientation at anthesis	
Filament colour	
Filament length	
Filament relative lengths	
Outer filament insertion	
Inner filament insertion	
Style orientation at anthesis	
Ovary shape	
Capsule shape	
Capsule orientation	
Capsule length	
Infructescence elongation	
Testa lustre	
Seed length	
Seed width	
Seed shape	
Testa primary sculpturing	
Testa secondary sculpturing	
Strophiole length	
Strophiole texture	
Strophiole inflation	
Raphe inflation	
Chalazal collar length	

Lachenalia is confined mainly to the winter rainfall zone of the subcontinent. Speciation in this genus is probably the result of isolation and genetic drift in combination with natural selection. Phenotypic expression across populations can also be influenced by founder effect, in which the founder population is morphologically distinct due to the restricted genotypes of pioneering individuals. Populations of fewer than approximately 50 effectively breeding individuals are at increased risk of fixation of alleles and loss of diversity due to inbreeding (Richards 1986). Similarly, evolutionary bottlenecks, in which there is a sudden decrease in population size, with a corresponding reduction of genetic variability, reduces heterozygosity of populations.

In addition to phenotypic plasticity, polymorphism is also encountered in *Lachenalia*. While phenotypic plasticity refers to the variability of expression of characters due, for example, to environmental conditions, polymorphism refers to the sympatric presence of two or more distinct morphological expressions within different individuals of a species.

6.3 DESIGNATION OF RANKS

6.3.1 Species, subspecies and varietal rank

The current study provides a record of intraspecific and interspecific variation in *Lachenalia* and *Polyxena* across its wild distribution range as well as under cultivation. For this purpose it was necessary to distinguish between phenotypic and genotypic variation and to define characters and character states which were found to be reasonably constant. In this study, a combined total of one hundred and thirty-nine taxa were recognised in *Lachenalia* and *Polyxena*. These comprised one hundred and fifteen *Lachenalia* species including six subspecies and twenty-four varieties, and five *Polyxena* species. Five of the nine new species recognised (*L. arida*, *L. canaliculata*, *L. lutea*, *L. nardouwensis*, *L. urceolata*) were previously regarded as morphological forms of other species, while the remaining four were completely new (*L. cernua*, *L. fasciculata*, *L. komsbergensis*, *L. wiesei*). A new subspecies

(*L. undulata* subsp. *grandifolia*) was based on leaf morphology and distribution data. The four new varieties were based on floral and distribution data (*L. aloides* var. *bonaspei*, *L. aloides* var. *piketbergensis*, *L. aloides* var. *thunbergii*, *L. contaminata* var. *exserta*). The two new combinations included the elevation of an old species (*L. massonii*), placed in synonymy by a previous researcher (Barker 1980), to subspecific level under *L. trichophylla* on the basis of floral and leaf morphology, and distribution data, and a recently described variety (*L. violacea* var. *glauca*) being elevated to specific level, on the basis of floral and seed morphology, and distribution data. *L. pallida*, which was previously recognised as a distinct species (Aiton 1789), did not merit specific rank and was reassessed as a yellow-flowered form of the widespread and variable *L. pustulata*, based mainly on similarities in flower, leaf and seed morphology.

7 PHENOLOGY

7.1 FLOWERING AND LEAFING PERIOD

Collectively, the genus *Lachenalia* had a very long flowering period of almost twelve months *in situ* (depending on rainfall patterns), extending from mid-January and early February (*L. pearsonii*) until late December (*L. muirii*), with the largest number (88 taxa) in flower in September, and the lowest number (one taxon) in flower in January, February and March (Table 47). The collective leafing period for the genus was of slightly shorter duration and extended from mid-January until early November. The active growing season for all species except one (*L. pearsonii*) coincided with autumn and winter rainfall, both in winter and predominantly summer rainfall areas. Most species were synanthous, with the growth cycle characterised by rapid vegetative growth following the onset of cool wet weather from early to late autumn. The cold wet conditions from early to late winter were followed by flowering in mild, relatively moist weather from late winter to late spring. With the onset of summer, leaf and root senescence marked the beginning of a dormant period which lasted throughout the hot dry summer (Duncan & Anderson 1999). Under cultivation, two Eastern Cape endemics, *L. campanulata* and *L. convallarioides*, as well as *P. longituba* from the Komsberg in the Sutherland district, remained evergreen unless forced into dormancy by sustained drought.

Table 47. Flowering phenology in *Lachenalia* and *Polyxena*

TAXA/MONTHS	J	F	M	A	M	J	J	A	S	O	N	D
<i>L. orthopetala</i>									■	■		
<i>L. patula</i>									■	■		
<i>L. pearsonii</i>	■	■										
<i>L. peersii</i>										■	■	
<i>L. peeryae</i>							■	■	■			
<i>L. physocaulus</i>								■	■			
<i>L. polyphylla</i>										■	■	
<i>L. polypodantha</i>								■	■			
<i>L. purpureocaerulea</i>									■	■	■	
<i>L. pusilla</i>				■	■	■						
<i>L. pustulata</i>								■	■	■		
<i>L. reflexa</i>						■	■					
<i>L. rosea</i>								■	■	■	■	■
<i>L. rubida</i>			■	■	■	■	■					
<i>L. salteri</i>									■	■	■	■
<i>L. sorgeantii</i>										■	■	
<i>L. schelpii</i>							■	■	■			
<i>L. splendida</i>							■	■	■			
<i>L. steyneri</i>								■	■	■		
<i>L. thomasiiae</i>									■	■	■	
<i>L. trichophylla</i> subsp. <i>trichophylla</i>								■	■	■		
<i>L. trichophylla</i> subsp. <i>massonii</i>								■	■			
<i>L. undulata</i> subsp. <i>undulata</i>					■	■						
<i>L. undulata</i> subsp. <i>grammifolia</i>					■	■						
<i>L. unicolor</i>									■	■	■	
<i>L. unifolia</i> var. <i>unifolia</i>								■	■	■	■	
<i>L. unifolia</i> var. <i>schlechteri</i>								■	■	■	■	
<i>L. urceolata</i>							■	■	■			
<i>L. valerieae</i>						■	■					
<i>L. variegata</i>								■	■	■	■	
<i>L. ventricosa</i>							■	■	■			
<i>L. verticillata</i>								■	■	■		
<i>L. violacea</i>								■	■	■	■	
<i>L. viscidiflora</i>						■	■	■				
<i>L. whitethillensis</i>									■	■	■	
<i>L. wiesei</i>						■	■	■				
<i>L. xerophila</i>							■	■	■	■	■	
<i>L. yungii</i>							■	■	■	■	■	■
<i>L. zebrina</i>								■	■	■	■	
<i>L. zeyheri</i>								■	■	■	■	
<i>P. corymbosa</i>				■	■	■						
<i>P. ensifolia</i>				■	■	■						
<i>P. longintha</i>				■	■	■						
<i>P. maughanii</i>					■	■	■					
<i>P. panicifolia</i>				■	■	■						

The leaves of the earliest-flowering species (*L. pearsonii* and *L. rubida*) were almost always partially hysteranthous. These two species usually entered dormancy from late winter to mid-spring, much earlier than the winter-, spring- and early summer-flowering species. A group of ten *Lachenalia* species (*L. angelica*, *L. comptonii*, *L. isopetala*, *L. liliiflora*, *L. macgregoriorum*, *L. muirii*, *L. nervosa*, *L. orthopetala*, *L. peersii*, *L. purpureocaerulea*) were proteranthous *in situ*, as their flowers appeared at the end of the growing season in summer, after the leaves had withered (Duncan 1987, Duncan & Linder Smith 1999b). Only *L. pearsonii* from inland southern Namibia followed a summer-rainfall growth cycle in the wild, and normally flowered in January and February at the hottest time of year following late summer rains, and entered dormancy in late winter. However, this species is opportunistic in an area of extremely erratic rainfall, and in cultivation it readily adapted to a winter growth cycle. Two *Lachenalia* species from the mountains of the southern Cape, *L. montana* and *L. sargeantii* were wholly dependent on summer fires for flowering to occur (Duncan 1998b). The flowering performance of numerous *Lachenalia* species including *L. rosea*, *L. peersii* and *L. salteri* was greatly enhanced by fire but was not dependent on it for flowering to occur (Duncan 2003c, d, Duncan & Anderson 1997). In all *Polyxena* and most *Lachenalia* species, the leafing period was directly correlated to the main rainy season. Several species which occur in mainly summer-rainfall regions still followed a winter-rainfall growth cycle. Thus *L. karooica* from southwestern Free State, the eastern parts of the Northern Cape and the northwestern parts of the Eastern Cape grows from April to September and flowers from June to September; *L. convallarioides* from the eastern part of the Eastern Cape grows from April to November and flowers in late September and October, and the high altitude species *L. campanulata* from the mountains of the Eastern Cape interior grows from February to December and flowers from October to December (Duncan 1998b).

Phenology is important in maintaining species barriers where taxa are sympatric. Flowering and growth periods are greatly influenced by prevailing weather conditions, and flowering periods of variable species like *L. aloides* and *L. bulbifera* extend over periods of up to six months. This instability meant that phenological characters could not be included in the

cladistic analyses.

8 POLLINATION BIOLOGY

Floral characters may be associated with specific pollination systems and this implies the presence of functionally correlated suites of characters, often recognised as pollination syndromes (Bruneau 1997). Breeding systems of the genus were not examined in detail, but floral divergence appears to be driven by adaptation to a number of vectors and therefore pollination observations and putative syndromes are outlined below. Pollination type was not used in the cladistic analyses but several floral characters, potentially associated with pollination syndromes, such as flower shape and perianth tube length were included. The following casual observations have been made on animal visitors to *Lachenalia* populations over a period of six years. The observations are not substantiated by statistics or insect vouchers as this was not the focus of the current project.

Most of the species were self incompatible. However, two unusual *Lachenalia* species with subcapitate racemes (*L. barkeriana*, *L. pusilla*) and one *Polyxena* species with corymbose racemes (*P. longituba*) showed a breakdown in self incompatibility and set copious amounts of seed regardless of animal visits. Cultivated specimens of these three species in tight bud stage were placed under windless, isolated indoor conditions at Kirstenbosch Botanic Garden for the duration of the flowering period, and were subsequently monitored indoors to determine whether any seedset occurred; all three species produced copious amounts of seed. Five other *Lachenalia* species (*L. contaminata*, *L. juncifolia*, *L. lactosa*, *L. nervosa* and *L. reflexa*) as well as *P. ensifolia* and *P. maughanii* produced a heavy seedset under cultivation without any obvious evidence of cross-pollination.

The differences in floral structure in *Lachenalia* are adaptations to a variety of pollination and seed dispersal strategies. The flowers attract their pollinators primarily by colour, fragrance and shape, and offer rewards of nectar and pollen. Two strongly selected pollination syndromes were encountered in *Lachenalia*, namely mellitophily and ornithophily. Generalist flower visitors were foraging wasps and the Painted Lady butterfly (*Vanessa cardui* (L.)). Rodent

pollination is a probable but as yet unconfirmed pollination mechanism for two species of *Lachenalia* (*L. barkeriana*, *L. pusilla*).

8.1 MELLITOPHILY

Honey bees (*Apis mellifera* (L.)) belonging to the family Apidae: Anthophorinae visited the tubular flowers in all species of *Polyxena*, all of which were scented. They also visited the full range of flower shapes in *Lachenalia*, with the exception of the species with unscented long, tubular, brightly coloured flowers, which were pollinated exclusively by sunbirds. Specialisation for bee pollination in *Lachenalia* includes mechanically strong flowers with adequate landing facilities and a tepal surface that provides an adequate foothold (Faegri & van der Pijl 1979). The anthers of bee-pollinated species were prominent and usually bright yellow. Bees are attracted to colour, and also to scent, which was emitted, to a greater or lesser degree, in all bee-pollinated species. Certain species of *Lachenalia* were heavily scented, such as *L. fistulosa* (very sweetly scented) and *L. glauca* (heavily coconut-scented) (Duncan 1988a), and *L. nervosa* (scented like a mixture of cloves and carnations) (Duncan & Linder Smith 1999b) and *L. peersii* (scented like carnations) (Duncan 2003c). *P. corymbosa* and *P. paucifolia* were honey-scented, and the remaining three *Polyxena* species had a spicy scent (Duncan 2003a). Bees alighted on the lower inner tepals of species with oblong-campanulate flowers including *L. mathewsii*, *L. physocaulos*, *L. purpureocaerulea* and *L. pustulata*, entered the flower and collected nectar, then either collected pollen or left the flower. Pollen deposition was nototribic. In leaving the flower the bee usually brushed against the stigma. Vogel (1954) pointed to the specialised floral ecology of one species, namely the mellitophilous brush mechanism of the geoflorous *L. pusilla* (which also applies to *L. barkeriana* and *P. ensifolia*), in which the exerted, erect stamen filaments act as the main visual attraction of the flowers. In the outgroup (*Massonia*) the flowers also had prominent filaments, and most species were visited by honeybees, except in *M. depressa* which is specialised for rodent pollination (Johnson *et al.* 2001).

Anthophorid bees belonging to the family Apidae: Anthophoridae fed on the nectar of two

populations of *L. pustulata* on the Cape west coast at Saldanha and Vredenburg. Honey-bees and foraging wasps visited the flowers of *Lachenalia* and *Polyxena* from mid-morning (from 10 a.m. onwards) until mid-afternoon (up until about 3 p.m.), while anthophorid bees were most active from early to mid-morning between 8 a.m. and 11 a.m.

8.2 ORNITHOPHILY

Lachenalia species with unscented, brightly coloured tubular flowers with long perianth tubes and an abundance of nectar (*L. aloides*, *L. bulbifera*, *L. reflexa*, *L. rubida* and *L. viridiflora*) conform to the bird pollination syndrome (Faegri & van der Pijl 1979; Proctor & Yeo 1972). *L. algoensis* probably also forms part of this syndrome. These species all appear specialised for pollination by sunbirds (*Nectariniidae*), notably lesser double-collared sunbirds, *Nectarinia chalybea* (L.), which occur throughout their distribution range. The flowers of these species are mainly shades of yellow, orange, red and pink, i.e. *L. bulbifera* (yellow, bright red or orange), *L. rubida* (bright pink), *L. reflexa* (bright yellow) and *L. aloides* (bright yellow or orange, or a combination of different bright colours). The bright turquoise flowers of *L. viridiflora* are also pollinated by lesser double-collared sunbirds (Manning 2000). The bright yellow flowers of *L. reflexa* and the turquoise flowers of *L. aloides* var. *vanzyliae* are probably also pollinated by this species (Duncan & Anderson 2003). The flowers of *L. algoensis* vary in shades of yellow. Most of the sunbird-pollinated species have peduncles which are strong enough for visiting sunbirds to cling to while probing the perianth tubes for nectar. *L. viridiflora* and *L. reflexa* are anomalous in having rather short, weak peduncles and their sunbird pollinators have to probe the flowers directly from the ground. Illustrating the convergent adaptation of flowers to similar pollinators, the long perianth tube and tubular perianth of the putatively sunbird-pollinated *L. reflexa* are similar to other sunbird pollinated species, but the erect or suberect flower orientation in this species and in *L. viridiflora*, and the construction of the tubular perianth in *L. reflexa* differs in that it narrows distinctly towards the mouth, compared with the pendulous or cernuous flowers and absence of narrowing of perianth segments in all other sunbird pollinated species. When feeding on the species with

sturdy peduncles, the sunbird clings to the base of the peduncle and inserts its curved beak into the tubular, pendulous perianth, in so doing lifting the perianth into a spreading position. Sunbirds visit the flowers of *L. aloides* var. *aloides*, *L. aloides* var. *quadricolor*, *L. bulbifera* and *L. rubida* from early morning around 8 a.m. until late afternoon around 5 p.m.

8.3 RODENT POLLINATION

The ground-level flowers of *Massonia depressa* (a member of the outgroup genus used in the cladistic analyses in this thesis) emit a strong yeasty odour and have been shown to be pollinated at night by at least four rodent species, including two gerbil species in the Succulent Karoo in the northwestern Cape (Johnson *et al.* 2001). The possibility exists that the ground-level flowers of *L. barkeriana* and *L. pusilla* are also pollinated by rodents as their flowers emit an extremely strong yeasty odour, much stronger than that of *M. depressa*, and *L. barkeriana* and *M. depressa* occur in similar Succulent Karoo habitat. *L. barkeriana* and *L. pusilla* are the two species with the shortest flowering period (no more than two weeks) of all the *Lachenalia* species.

9 PHYTOGEOGRAPHY

9.1 MATERIALS AND METHODS

Data were obtained for all 115 *Lachenalia* and five *Polyxena* species currently recognised, in quarter degree and full degree grid square increments. Repeat data were eliminated, and the species totals placed on relevant grid squares on maps of southern Africa (Figures 46, 47). A table of the ten most speciose quarter degree grids for *Lachenalia* was drawn up (Table 48).

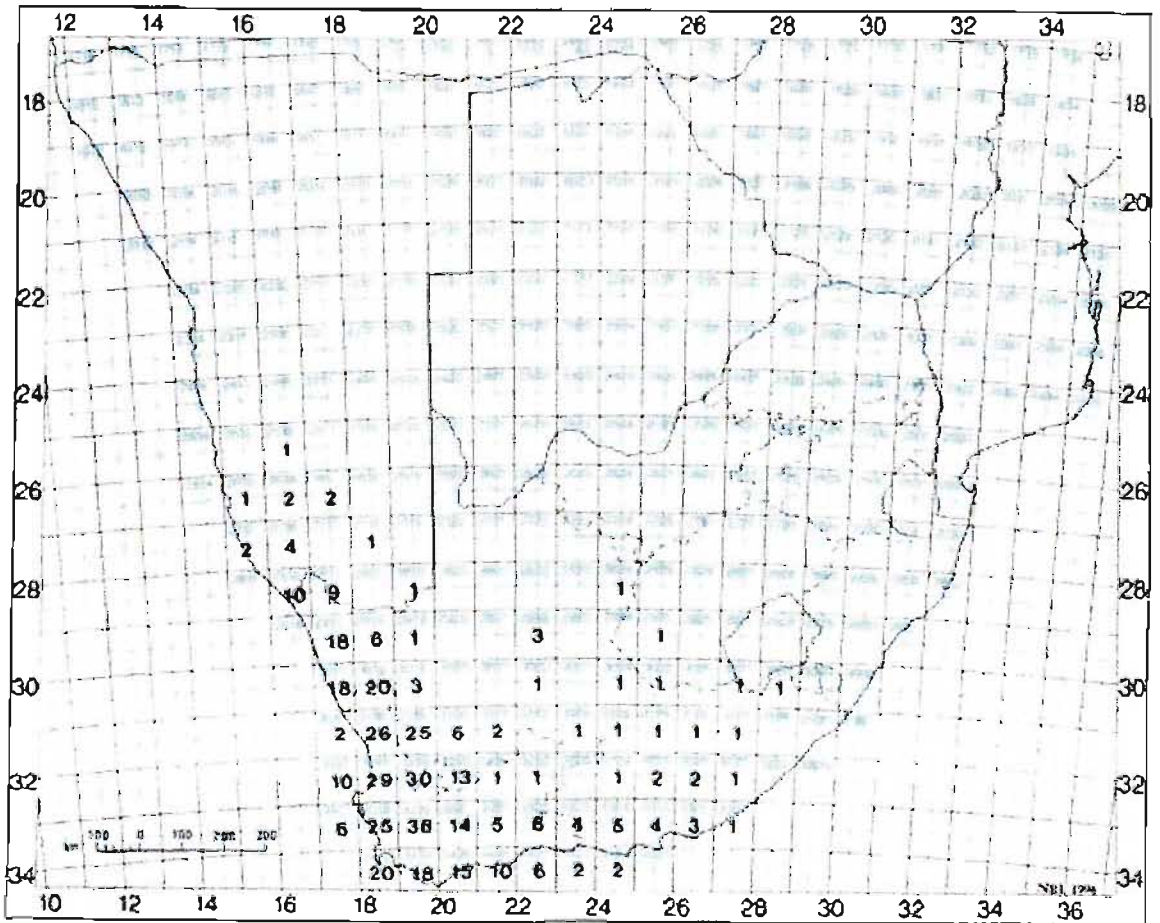


Figure 46. Species richness in *Lachenalia* in geographical degree squares.

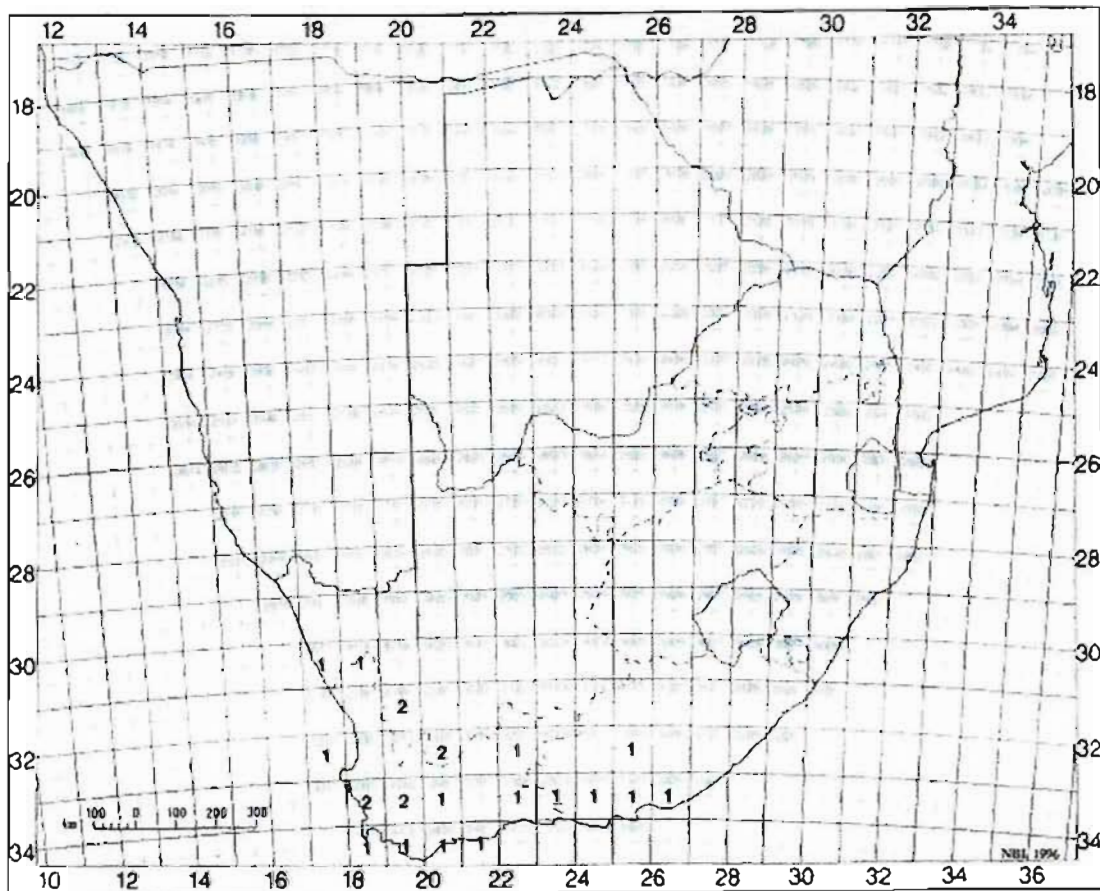


Figure 47. Species richness in *Polyxena* in geographical degree squares.

Table 48. Ten most speciose quarter degree squares for *Lachenalia*

Grid Square	Region	Number of species
3318 DA	Philadelphia	15
3119 AC	Nieuwoudtville	14
3318 CD	northern Cape Peninsula	14
3318 DC	Bellville	14
3418 AB	southern Cape Peninsula	13
3218 BB	Clanwilliam	13
3219 AA	Pakhuis	12
2917 DB	Springbok	11
3319 BC	De Doorns	11
3217 DD	Vredenburg	10

9.2 DISTRIBUTION

The three most northerly records for *Lachenalia* were from Namibia; *L. arida* from the farm Tsiras, +/- 35 km south of Helmeringhausen in southwestern Namibia (2516 DD), *L. giessii* from Garub, west of Aus (2616 CA), and *L. nutans* from Haalenberg, east of Lüderitz (2615 DA). *L. pearsonii* occurred furthest inland in Namibia on Lord Hill in the Great Karasburg Mountains in southern Namibia (2718 BA). *L. karooica* occurred the furthest inland in South Africa on the farm Wolwefontein at Barkly West (2824 DA), northwest of Kimberley in the Northern Cape, and further southwest between Campbell and Schmidtsdrift (2824 CA). The genus was also represented in the Free State by *L. karooica* at Fauresmith (2925 CB). The most easterly record was that of *L. campanulata* from Ongeluks Nek, west of Matatiele, close to South Africa's border with southeastern Lesotho (3028 AD).

The most northerly record for *Polyxena* was that of *P. ensifolia* from Studer's Pass, west of Garies, in southwestern Namaqualand (3017 AD), and also occurred the furthest inland at Voëlfontein farm northwest of Sutherland in the southern Great Karoo (3220 AB). The most easterly record for *Polyxena* was that of *P. ensifolia* at Bathurst in the Eastern Cape (3326 DB) (Van der Merwe 2002).

The main centre of diversity for *Lachenalia* was divided between the Succulent Karoo and Fynbos biomes in the 3319 (Worcester) grid, in the valleys and flats of the interior mountains of the winter rainfall region of the southwestern Cape, where 38 species occurred (Figure 46). This grid contained a relatively high number of species restricted to just one known locality, or which had extremely limited ranges. Within this grid, the largest number of species per quarter degree square occurred in the 3319 BC grid, located in the De Doorns area of the Worcester-Robertson Karoo, where 11 species occurred (Table 48). The quarter degree square with the most species was 3318 DA (Philadelphia) in the southwestern Cape, with 15 species (Table 48). There was a marked decrease in species diversity towards the summer rainfall areas of the eastern and northeastern parts of the Eastern Cape, the Great

Karoo (particularly in the vast southern part known as Die Vlakke), Bushmanland, and the southeastern parts of Namibia.

There were no records of *Lachenalia* from the 3122 and 3223 degree squares of the Great Karoo, but this was probably due to undercollecting. *L. karooica* occurred in several widely separated localities in mainly summer rainfall areas of the northwestern parts of the Eastern Cape, southwestern Free State and northeastern Northern Cape, with an outlier at Prieska in central Northern Cape. Similarly, *L. bowkeri* had an almost exclusively Eastern Cape distribution, with an outlier west of Colesberg in the northeastern Great Karoo, a disjunction of more than 200 km. The deciduous nature of the genus, inhospitable terrain and the fact that growth and flowering are dependent on sufficient seasonal rainfall, were contributory factors to poor distribution records for these areas (Duncan 1999).

P. ensifolia had the widest distribution of the five *Polyxena* species, and was the only species represented in the south-central and near-eastern parts of South Africa (Figure 47).

9.3 FACTORS PROMOTING SPECIATION AND DISTRIBUTION

The two most important modes of speciation in *Lachenalia* appear to have been allopatry and ploidy changes.

Evolution under circumstances of environmental change such as increasing aridity, tends to increase in areas of moderate to low precipitation, where species on the margins of their distribution range may become isolated due to the development of physical barriers disrupting gene flow (like mountain ranges, or to unfavourable environmental conditions). This results in populations becoming reproductively isolated and diverging morphologically, leading to allopatric speciation (Stebbins 1952, Axelrod 1972). Speciation can also occur through founder populations as a result of extraordinary long-distance dispersal of seed beyond the normal gene flow range of the parent population. Differing circumstances of environmental change on the parent and founder populations in conjunction with random genetic drift may

result in morphological divergence of the founder population, and eventual speciation.

Africa's arid regions are thought to be of considerable age due to their high biodiversity (Jurgens 1997). Many geophytic genera have speciated extensively in the arid southern and western parts of the subcontinent. Goldblatt (1978) and Axelrod & Raven (1978) note that geographic speciation in this area is likely to have been rapid, and that much of the richness at the species level is of recent origin leading to high species : genus ratios. According to Linder (1985) divergence can occur across quite short time periods in the presence of sufficiently strong selective pressures. In *Lachenalia*, the arid regions of the Worcester-Robertson Karoo, Little Karoo, Ceres Karoo, Knersvlakte and central Namaqualand, as well as the semi-arid coastal regions of the southwestern and western Cape have given rise to high levels of speciation. Almost all the *Lachenalia* species occurring in these regions are endemic, implying local radiation. Similarly, three of the five *Polyxena* species have extremely localised ranges. Considering the large numbers of closely related *Lachenalia* species typical of these highly diversified lineages, much speciation is probably recent. Speciation in *Lachenalia* has given rise to arid-adapted features aimed at the reduction of water loss during the growing period and the protection of the bulb during the dormant period. As an example, on the barren Knersvlakte in southern Namaqualand, leaf and bulb reduction is clearly evident in the endemic *L. patula*. Its extremely succulent, short subterete leaves are able to store large quantities of water and it has the smallest bulb of all the *Lachenalia* species, surrounded by extremely tough, cartilaginous outer scales.

Disjunct populations often represent the initial stages of microspeciation. The large topographical diversity present in southern Africa has given rise to highly variable climatic conditions, superimposed upon very different soil types, which generates a wide range of spatially disjunct niches. Species richness in the geophyte flora in the region is a product of these factors (Cowling *et al.* 1989, Goldblatt 1978, Oliver *et al.* 1983), to which *Lachenalia* has successfully adapted.

Several widely distributed species occur across markedly different soil types. *L. unifolia*, which occurs in deep, acid sandy granitic or sandstone soils over much of the western parts of its range along the Cape west coast, is also found in alkaline, stony clayey soils in the valleys of the Little Karoo. Similarly, the widely distributed *L. bulbifera* occurs on deep alkaline sand dunes and flats, as well as on acidic, humus-rich loam on granite outcrops on the Cape west coast. *L. rubida* occurs on alkaline sand just above sea level on the Cape west coast and on acid sandstone outcrops on the southern Cape Peninsula. The widespread *P. ensifolia* occurs in stony, poorly drained clay soils in the western parts of its range and on granitic, well drained soils in the southern parts of its range. The variable *L. aloides* is always associated with rocky habitats in sandy loamy soils, and occurs in three different vegetation types, Fynbos, Coastal Fynbos and Strandveld. Many species appear to be edaphic neoendemics such as :

L. salteri which only occurs in seasonal bogs in acid sandstone of the southern Cape;

L. patula and *L. splendida* which only occur on quartzite flats and slopes of the Knersvlakte;

L. doleritica which only occurs in heavy, fine-grained doleritic clay on the Bokkeveld Plateau;

L. karooica which is restricted to dolomitic limestone outcrops belonging to the Ecca Shales of the Karoo System in the Northern Cape, Free State and Eastern Cape, and

L. alba, the Bokkeveld endemic, which only occurs in Dwyka Tillite, a hard stony clay soil belonging to the Karoo System, in renosterveld vegetation.

Geographic speciation and radiation in *Lachenalia* was intense in the southwestern and western parts of the distribution range, which form the most speciose centres for the genus. This was probably a direct consequence of allopatric speciation, where disruption of gene flow occurred due to spatial separation as a result of geographic barriers such as mountain ranges. The 3319 (Worcester) grid had the highest concentration of *Lachenalia* (38 species) in the flats and valleys created between major mountain ranges such as the Hex River Mountains and the Skurweberge, with their accompanying edaphic and microclimatic

variation. This phenomenon was also evident in the second- and third- most speciose areas for the genus, the 3219 (Wuppertal) grid (30 species) and the 3218 (Clanwilliam) grid (29 species), where disruption of gene flow created by major mountain ranges like the Cederberg, Koue Bokkeveld, Olifantsrivierberge and Piketberg ranges has occurred.

In her cladistic study of evolution and homology of bird pollination syndromes in *Erythrina* (Leguminosae), Bruneau (1997) noted that contrary to the notion of Ornduff (1969) and Wyatt (1988) that characters associated with pollination systems were thought to provide biased assessments of phylogenetic relationships in angiosperms, her analysis suggested that when syndromes are dissected into their component cladistic characters, these characters provide hypotheses of homology for evaluating phylogenetic relationships that are independent of pollination biology. In the present study, flower colour and pollination syndromes were not used as characters in the cladistic analyses.

In their analyses of adaptive radiation and topology of large phylogenies, Guyer & Slowinski (1993) define adaptive radiation as some organisms having features that allow them to speciate more prolifically or become extinct less frequently than organisms without these features. They further state that if this type of adaptive radiation was a consistent feature of evolution, then large phylogenetic trees should be significantly unbalanced.

10 PHYLOGENY

Darwin's (1859) evolutionary theory strove to classify taxa according to natural (phylogenetic) relationships, as opposed to the artificial, pre-Darwin classification systems. Cladistics is used to reconstruct genealogies of organisms, and to construct natural classifications based on ancestry, following the pioneering work of Hennig (1966). Several computer programs have been developed in order to analyse cladistic data sets, of which Hennig86 and PAUP* (Phylogenetic analysis using parsimony *and other methods) are the most widely used.

10.1 MATERIALS AND METHODS

10.1.1 Characters

A morphological cladistic analysis of species relationships in the genera *Lachenalia* and *Polyxena* has not previously been attempted. Morphological characters can be of two kinds, either discrete (qualitative) or continuous (quantitative) (Scotland 1992). Seventy-three characters comprising fifty-seven discrete and sixteen continuous characters were defined in *Lachenalia* and *Polyxena* (Appendix 1). Thirty-seven binary and thirty-six multistate characters were coded in the matrix. Characters were polarised using the outgroup comparison method to postulate the direction of evolutionary change, by assigning numerical values to each hypothesized character state change, with zero indicating the outgroup state, and values above zero indicating the derived state(s) (Appendix 2). Character states were unordered, autapomorphies were excluded (because they provide no grouping information), and unknown character states were indicated by a question mark (?). The endemic southern African *Massonia depressa* was chosen as the outgroup. It forms part of the tribe Massonieae recognised by Pfosser & Speta (1999) and Pfosser *et al.* (2003), and shares the most recent common generic ancestor with *Lachenalia* and *Polyxena*, according to the molecular phylogenies of Wetschnig *et al.* (2002) and Manning *et al.* (2004).

10.1.2 Cladogram construction

The computer program PAUP* (Version 4.0b10) was used for the cladistic analyses (Swofford 1999). Due to the large data set (139 taxa comprising the ingroup, one taxon comprising the outgroup) and the relatively few (73) morphological characters, the heuristic method was used to search for the most parsimonious trees. This method does not guarantee to find the optimum trees, but cuts down on prohibitive computer time. Even if very extensive searches are conducted, there is still no certainty that the shortest trees have been found. In the heuristic method, two strategies are used, stepwise addition and branch swapping. In stepwise addition, an initial tree is obtained which operates by connecting taxa, one at a time, to a developing tree until all taxa have been joined. In branch swapping, the tree is subjected to multiple rearrangements in order to address parsimony.

Using the data matrix for all *Lachenalia* and *Polyxena* taxa listed in Appendix 2, an initial parsimony analysis was performed in which all 73 characters were unordered and unweighted, with the trees rooted using the outgroup comparison method (Analysis 1). During stepwise addition, starting trees were obtained using random addition sequences. One thousand replicates were performed, with five trees held at each step. For character-state optimization, the delayed transformation (DELTRAN) method was employed.

To establish a measure of confidence in the results of the unweighted analysis (Analysis 1), a bootstrap analysis was performed on 1000 replicates, using a heuristic search.

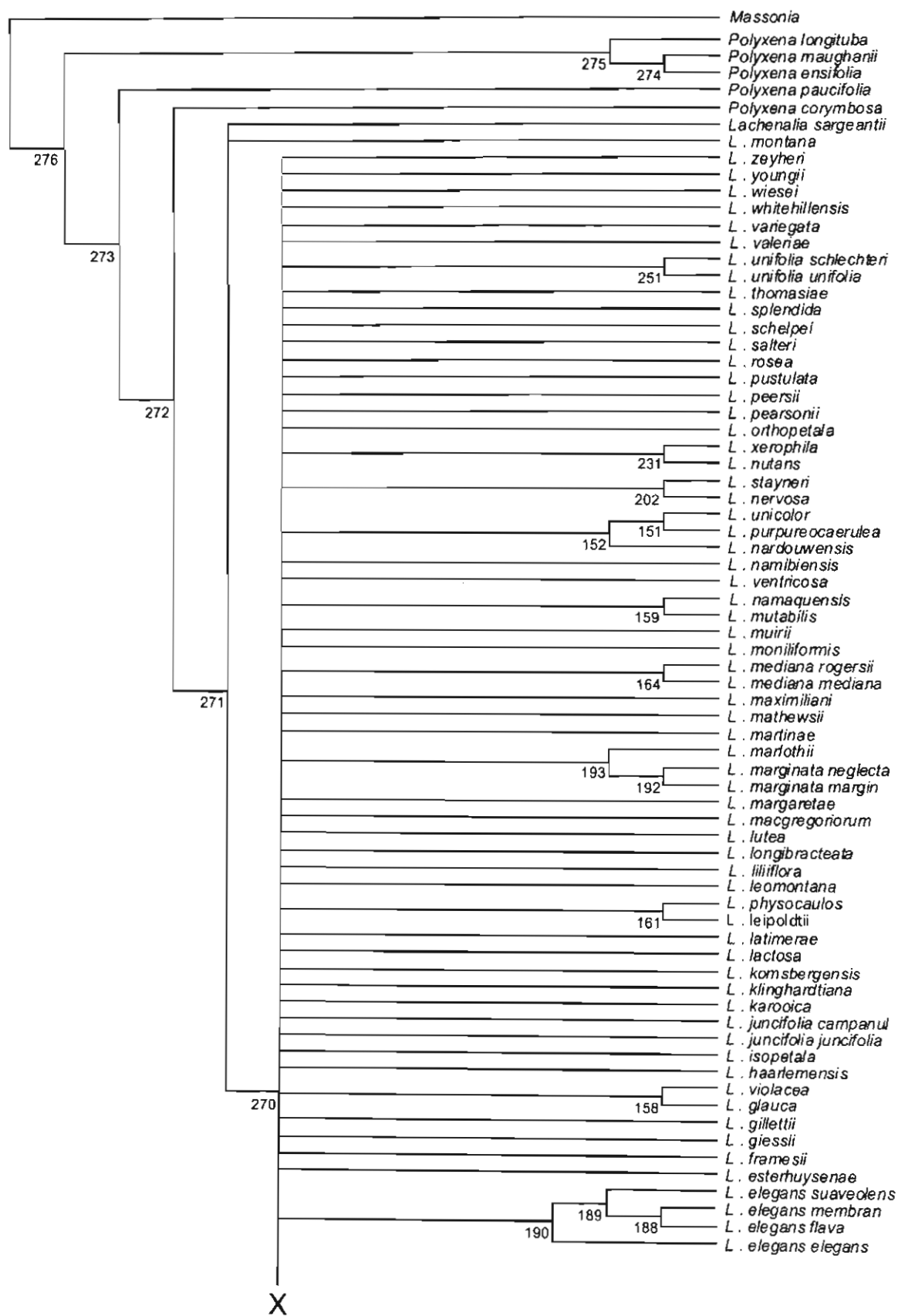
Due to the high level of homoplasy present in the unweighted trees in Analysis 1, a weighted analysis using successive approximations character weighting (SACW) was performed, in an attempt to resolve some of the homoplasy (Analysis 2). The successive weighting scheme assigns relative ranks to characters, such that characters with more informative features are valued higher than others, thereby reducing the influence of the most homoplasious characters.

As in Analysis 1, all 73 characters were unordered, with the trees rooted using the outgroup comparison method. Starting trees were obtained via stepwise addition using a random addition sequence, and 1000 replicates were performed, with five trees held at each step. For character-state optimization, the delayed transformation (DELTRAN) method was employed.

10.2 RESULTS AND DISCUSSION

10.2.1 Analysis 1.

Parsimony analysis generated 20 equally parsimonious trees of 930 steps, with a consistency index (CI) of 0.133, a homoplasy index (HI) of 0.867, a retention index (RI) of 0.629 and a rescaled consistency index (RC) of 0.084. The strict consensus of 20 equally parsimonious trees is shown in Figure 48.



X

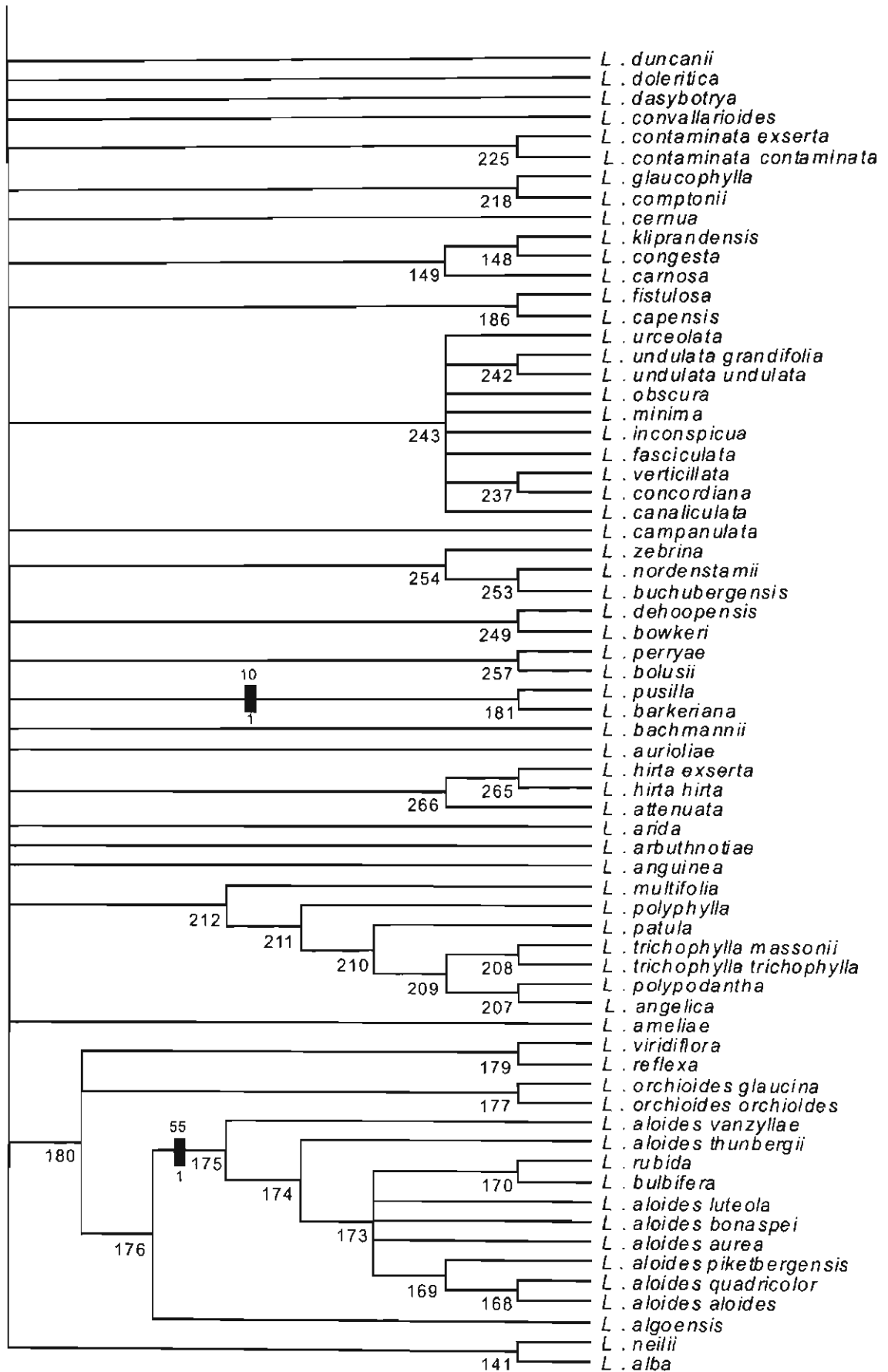
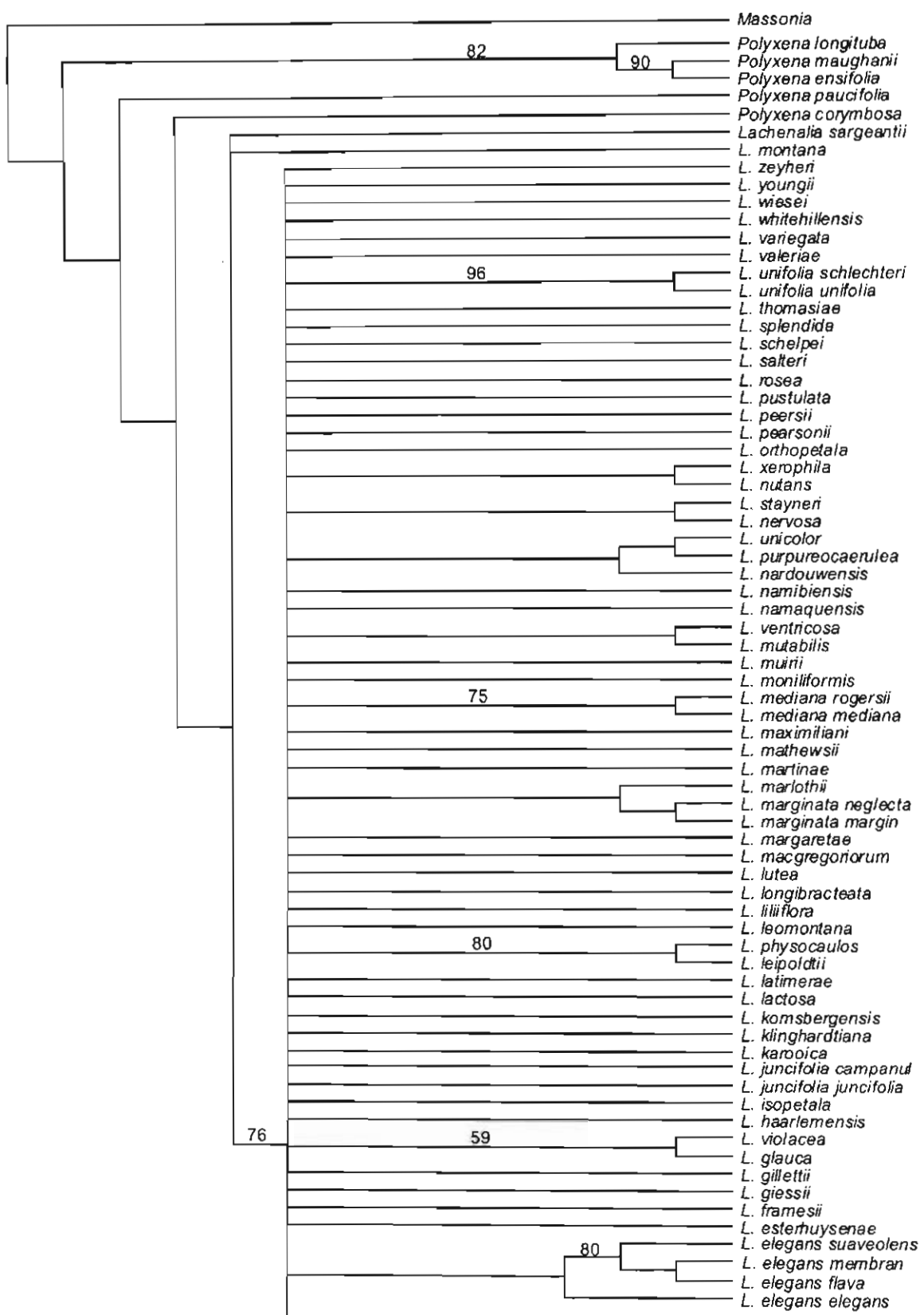


Figure 48, continued.

The results of the analysis suggested that the recognition of *Polyxena* as a separate genus renders *Lachenalia* paraphyletic. *P. longituba*, *P. ensifolia* and *P. maughanii* formed the basal clade, with *P. paucifolia* and *P. corymbosa* placed immediately above. The uppermost major clade containing most *Lachenalia* taxa was polychotomous, including a large number of unresolved taxa, numerous terminal species pairs, and several larger clades. Marked synapomorphies link a terminal clade at node 181 in which the sister species *L. barkeriana* and *L. pusilla* are supported by the common occurrence of concrescent leaf bases (character 10, state 1), and medial inner filament insertion at node 175 (character 55, state 1) which links all eight *L. aloides* varieties with *L. bulbifera* and *L. rubida*. The strict consensus tree showed a very low level of resolution and the character state reconstruction data generated from arbitrarily selected tree number one of 20 equally parsimonious trees indicated a high level of homoplasy across the tree, evident as numerous parallelisms and reversals. The bootstrap analysis indicated that most major nodes were unsupported, with highest support for nodes closer to the taxa. The bootstrap values are shown in the strict consensus tree in Figure 49.



X

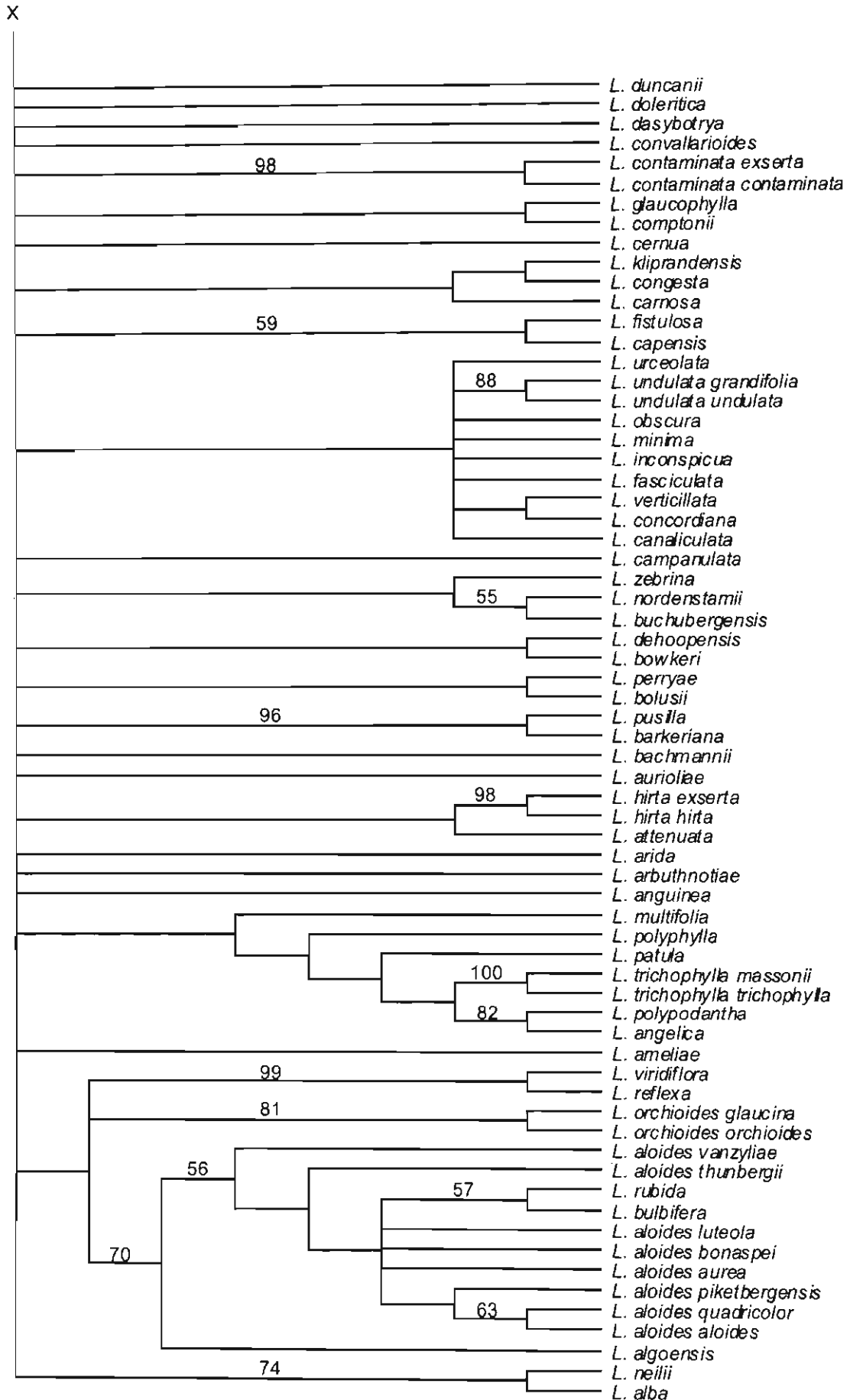
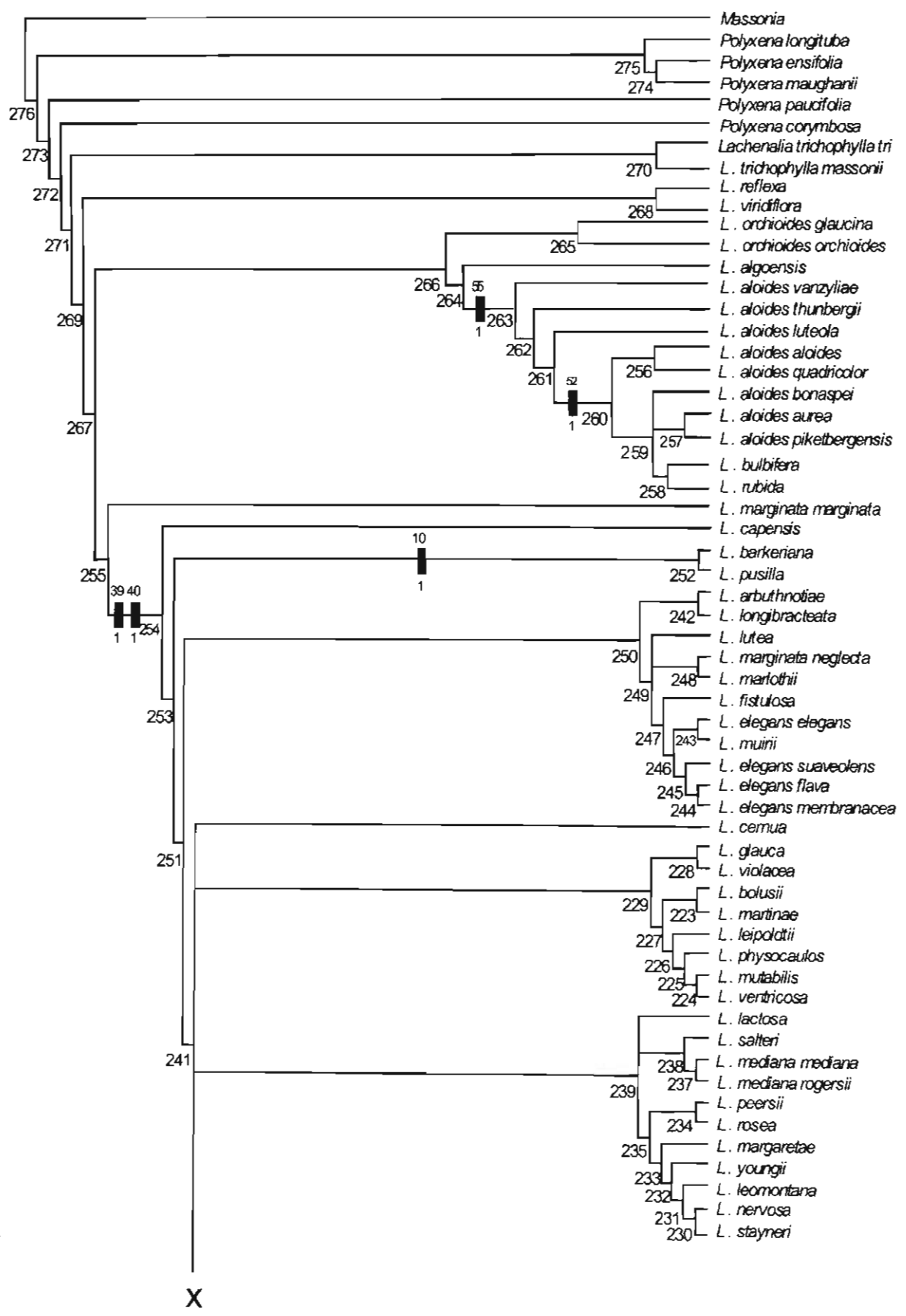


Figure 49, continued.

10.2.2 Analysis 2.

Parsimony analysis generated 10 equally parsimonious trees of 961 steps, with a consistency index (CI) of 0.129, a homoplasy index (HI) of 0.871, a retention index (RI) of 0.615 and a rescaled consistency index (RC) of 0.079. The strict consensus of 10 equally parsimonious trees is shown in Figure 50.



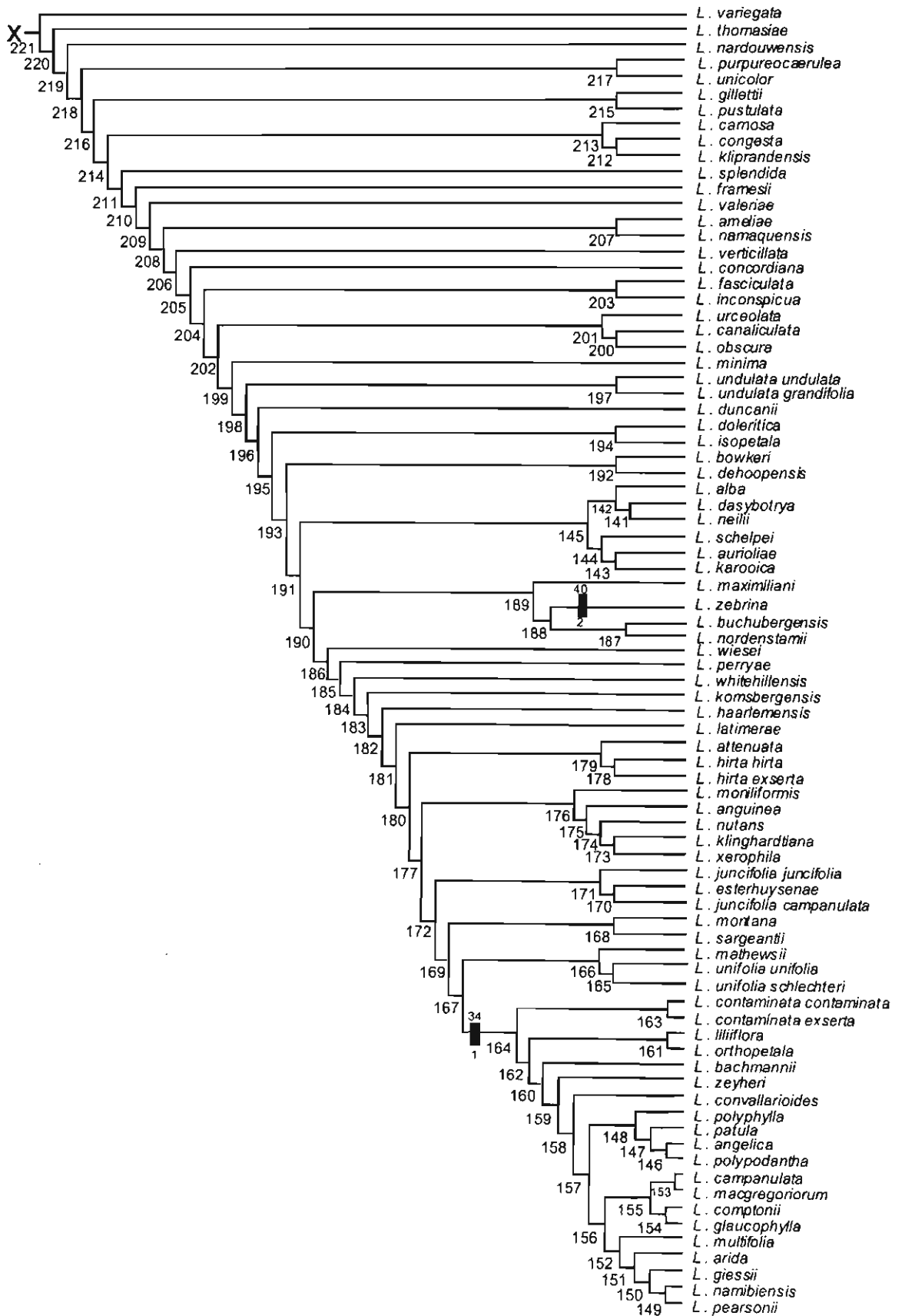


Figure 50, continued.

The strict consensus showed a greatly improved level of resolution compared with that of the unweighted consensus tree in Analysis 1. The major polychotomy in the unweighted analysis was resolved in the weighted analysis, but homoplasy remained at a high level. *Polyxena* remained embedded within *Lachenalia*, with *P. longituba*, *P. ensifolia* and *P. maughanii* forming the basal clade, and *P. paucifolia* and *P. corymbosa* placed immediately above. The reduction in value placed on highly homoplasious characters had the effect of repositioning the clades, resulting in a significantly altered tree topology. When the outgroup was disregarded, and the ingroup was treated as unrooted in both analyses, the relationships within the ingroup were apparent. In both analyses, similar well defined groups occurred, with the taxa placed next to or adjacent to one another, indicating no major conflict in the topologies of the two trees. Four additional synapomorphies were obtained in the weighted analysis. The two synapomorphies obtained in the unweighted analysis, concrescent leaf bases (character 10 state 1, node 252) and medial inner filament insertion (character 55 state 1, node 263), occur at slightly different node positions. Seven taxa (five *L. aloides* taxa, *L. bulbifera* and *L. rubida*) are united by long filaments at node 260 (character 52 state 1). Short perianth tubes at node 254 (character 39 state 1) are shared across 116 taxa. Cup-shaped perianth tubes at node 254 (character 40 state 1) link 115 taxa, and 20 *Lachenalia* taxa are supported by cup-shaped lower bracts at node 164 (character 34, state 1) in the uppermost portion of the tree.

The major polychotomy at node 270 in the uppermost part of the unweighted consensus tree (Figure 48) could be due to insufficient data because of the low number of available characters in relation to the number of taxa analysed. In many instances, the consensus trees of both analyses corroborate intuitive classifications in terms of the relationships between species, and in certain instances accord with the speculated alliances in their original diagnoses. All infraspecific taxa were grouped together or adjacent to one another in the unweighted consensus tree, with the exception of the *L. juncifolia* taxa that were unresolved. In the weighted consensus tree (Figure 50), most infraspecific taxa were grouped together or adjacent to one another, with the exception of *L. marginata* subsp. *marginata* that was

placed on a branch of its own at node 255, and *L. marginata* subsp. *neglecta* resolved as the sister taxon to *L. marlothii* at node 248. *L. esterhuysenae* is considered most closely related to, and possibly conspecific with, *L. juncifolia* var. *juncifolia*, and was included in this study because of its longer filaments and much longer pedicels, and because of its restriction to high altitude. It was unresolved in the unweighted consensus tree but in the weighted consensus tree it resolved as sister taxon to *L. juncifolia* var. *campanulata* at node 170, with *L. juncifolia* var. *juncifolia* placed on a branch immediately below at node 171.

The most significant of the two synapomorphies obtained in the unweighted analysis is medial inner filament insertion (character 55 state 1), and supports all eight infraspecific *L. aloides* taxa, *L. bulbifera* and *L. rubida*. This synapomorphy is probably linked to the specialised sunbird pollination syndrome. The terminal clade comprising the sister species *L. barkeriana* and *L. pusilla* is supported by the synapomorphy concrescent leaf bases (character 10 state 1), a specialisation of the bulb in which the bases of the foliage leaves of the previous growing season remain intact. In the weighted analysis the most significant of the additional four synapomorphies obtained are short perianth tubes (character 39 state 1) and cup-shaped perianth tubes (character 40 state 1). Both these synapomorphies are probably linked to specialisation for bee pollination. With the exception of *L. polyphylla* that has an oblong-campanulate perianth, all the taxa supported by the synapomorphy cup-shaped lower bracts (character 34 state 1) either have narrowly campanulate or widely campanulate perianths, and in most of these taxa the perianths are white. The significance of cup-shaped lower bracts in combination with narrowly campanulate and widely campanulate, white perianths could form part of pollinator attraction. The synapomorphy long filaments (character 52, state 1) is probably linked to the specialised sunbird pollination syndrome.

10.2.3 Homoplasy

Homoplasy is easily identified in characters which arise independently of other characters. The recognition of homoplasy where natural selection causes simultaneous state changes across a number of characters, is more difficult. The latter scenario is likely to occur in response to pollinators.

Characters used in the analyses were grouped into a table of vegetative and reproductive character sets, with the corresponding consistency index values obtained in each analysis (Table 49). The consistency index value obtained for each character provided a good indication of the level of homoplasy; the lower the consistency index, the higher the homoplasy level. A high level of homoplasy was indicated for most characters by the generally low consistency index values. The most homoplasious characters have clearly been highly influential in the trees but due to the very low level of resolution obtained in the unweighted consensus tree (Figure 48), characters were analysed according to the weighted consensus tree (Figure 50). Characters with similar consistency index values were examined to establish whether they were evolving at the same or similar points in the tree, in order to determine whether any pattern of evolution could be identified.

Table 49. Consistency index (CI) values for vegetative and reproductive character sets in *Lachenalia* and *Polyxena*

Character number	VEGETATIVE CHARACTERS	CI values	
		weighted analysis	unweighted analysis
1	Bulb shape	0.054	0.061
2	Bulb tissue colour	0.286	0.286
3	Bulbil production	0.333	0.333
4	Offset production	0.037	0.043
5	Bulb outer tunic texture	0.111	0.111
6	Bulb apex	0.100	0.111
7	Bulb apex outer tunics	0.167	0.167
8	Inner cataphyll apex shape	0.095	0.118
9	Inner cataphyll adhesion	0.059	0.069
10	Leaf bases	1.000	1.000
11	Leaf base markings	0.071	0.087
12	Leaf number	0.108	0.118
13	Leaf orientation	0.167	0.200
14	Pustulate/non-pustulate adaxial leaf	0.250	0.250
15	Adaxial leaf trichomes	0.500	0.667
16	Adaxial leaf maculation	0.056	0.065
17	Leaf shape	0.083	0.087
18	Distal lamina profile	0.057	0.069
19	Basal lamina profile	0.067	0.077
20	Adaxial leaf tertiary sculpturing	0.098	0.100
21	Abaxial leaf tertiary sculpturing	0.071	0.081
22	Leaf margin anatomy	0.133	0.138
23	Leaf margin shape	0.056	0.056
24	Leaf margin vesture	0.375	0.375
25	Leaf apex shape	0.083	0.091
26	Primary seedling leaf orientation	0.118	0.111
27	Primary seedling leaf shape	0.083	0.077
Character number	REPRODUCTIVE CHARACTERS	CI values	
		weighted analysis	unweighted analysis
28	Peduncle elevation at anthesis	0.333	0.333
29	Peduncle inflation	0.400	0.400
30	Rachis apical anthocyanins	0.125	0.111
31	Rachis apical carotenoids	0.333	0.333
32	Rachis apical chlorophylls	0.500	0.500
33	Rachis apex structural white	0.250	0.250
34	Lower bract shape	1.000	0.500
35	Upper bract shape	0.091	0.100
36	Inflorescence type	0.167	0.154
37	Pedicel orientation at anthesis	0.250	0.211
38	Perianth shape (tepal orientation)	0.174	0.154
39	Perianth tube length	1.000	0.250
40	Perianth tube shape	1.000	0.400
41	Flower arrangement	0.143	0.167
42	Outer tepal shape	0.167	0.167
43	Outer tepal length	0.333	0.333
44	Outer tepal apex	0.100	0.111

Table 49. Consistency index (CI) values for vegetative and reproductive character sets in *Lachenalia* and *Polyxena*

Character number	REPRODUCTIVE CHARACTERS	CI values	
		weighted analysis	unweighted analysis
45	Inner tepal shape	0.200	0.182
46	Inner tepal length	0.500	0.500
47	Inner and outer tepal arrangement	0.045	0.056
48	Floral symmetry	0.500	0.500
49	Ventral inner tepal extension	0.091	0.095
50	Filament orientation at anthesis	0.130	0.125
51	Filament colour	0.182	0.182
52	Filament length	1.000	0.500
53	Filament relative lengths	0.200	0.167
54	Outer filament insertion	0.667	0.667
55	Inner filament insertion	1.000	1.000
56	Pollen exine sculpturing	0.083	0.111
57	Style orientation at anthesis	0.071	0.067
58	Ovary shape	0.077	0.071
59	Capsule shape	0.231	0.214
60	Capsule orientation	0.143	0.118
61	Capsule length	0.500	0.333
62	Infructescence elongation	0.333	0.333
63	Testa lustre	0.062	0.071
64	Seed length	0.200	0.222
65	Seed width	0.167	0.200
66	Seed shape	0.125	0.105
67	Testa primary sculpturing	0.143	0.167
68	Testa secondary sculpturing	0.182	0.182
69	Strophiole length	0.105	0.095
70	Strophiole texture	0.333	0.143
71	Strophiole inflation	0.500	0.200
72	Raphe inflation	0.500	0.500
73	Chalazal collar length	0.111	0.125

10.2.3.1 Vegetative homoplasy

Bulb shape (character 1)

The weighted consensus tree (Figure 50) indicated that subglobose bulbs have evolved from globose bulbs on numerous independent occasions across the genus, in geographically widely separated areas. The character state change occurred 12 times (at nodes 274, 272, 234, 184, *L. bulbifera* at node 258, *L. arbuthnotiae* at node 242, *L. marginata* subsp. *neglecta* at node 248, *L. fistulosa* at node 247, *L. ventricosa* at node 224, *L. salteri* at node 238, *L. nervosa* at node 230, and *L. bowkeri* at node 192), with nine reversals. The trait occurs in the Namaqualand coastal plain, the Bokkeveld Plateau, and the northwestern, western, southwestern and southern parts of the Western Cape. Ovoid bulbs have evolved from globose bulbs in numerous widely separated areas. This switch in bulb shape occurred 12 times (at nodes 256, 197, 189, 144, *L. aloides* var. *piketbergensis* at node 257, *L. violacea* at node 228, *L. mediana* var. *rogersii* at node 237, *L. verticillata* at node 206, *L. fasciculata* at node 203, *L. doleritica* at node 194, *L. campanulata* at node 153 and *L. namibiensis* at node 149). The trait occurs in southern Namibia, the Richtersveld, Namaqualand, western Bushmanland, the western, central and southern Great Karoo, the western parts of the Western Cape, and in the Eastern Cape.

The evolution of subglobose bulbs from globose bulbs has occurred mainly in deep sandy soils, mainly in higher rainfall areas, whereas ovoid bulb shape has evolved mainly in stony, clay-based soils in arid habitats. Bulb shape appears to respond rapidly to changing environments. The occurrence of character state shifts at the varietal level is curious in *L. aloides* and *L. mediana*.

Bulb tissue colour (character 2)

In the weighted consensus tree (Figure 50), yellow bulb tissue has evolved from white bulb

tissue three times (at nodes 220 and 161, and *L. ventricosa* at node 224), with two reversals. The trait occurs in the northwestern and western parts of the Western Cape. The polymorphic condition has evolved from yellow bulb tissue in Namaqualand, where it occurs in *L. carnosa* at node 213. The adaptive value of bulb tissue colour is unclear and does not appear to correlate to habitat.

Bulbil production (character 3)

In the weighted consensus tree (Figure 50), soboliferous bulbs have evolved from non-soboliferous bulbs three times (*L. bulbifera* at node 258, *L. namaquensis* at node 207, and *L. moniliformis* at node 176). The trait occurs in Namaqualand, the western, southwestern and southern coastal parts of the Western Cape, and in the Little Karoo. Cowling & Pierce (1999) hypothesize that stolon formation in *L. namaquensis* is a defensive strategy to escape the attention of mole rats, this probably also applies to *L. bulbifera* and *L. moniliformis*.

Offset production (character 4)

The weighted consensus tree (Figure 50) suggested that offset-forming bulbs have arisen from solitary bulbs on numerous independent occasions across the genus, in geographically widely separated areas, seven times (at nodes 276, 201, 193, *L. mutabilis* at node 224, *L. namaquensis* at node 207, *L. minima* at node 199, and *L. namibiensis* at node 149), with 20 reversals. This character state occurs in southern Namibia, Namaqualand, the Bokkeveld Plateau, the western, southwestern and southern parts of the Western Cape, and in the Eastern Cape. Most species that are offset-forming occur in higher rainfall areas, whereas those with solitary bulbs appear to have evolved almost exclusively in arid areas such as southern Namibia, the Richtersveld, western Bushmanland, Namaqualand, the central and western Great Karoo, and the Little Karoo.

Bulb outer tunic texture (character 5)

In the weighted consensus tree (Figure 50), spongy outer tunics have evolved from cartilaginous tunics three times (at nodes 276 and 191, and *L. inconspicua* at node 203), with five reversals. Taxa with spongy outer tunics occur across the genus in geographically widely separated areas and in widely differing habitats, whereas most taxa with hard outer tunics are restricted to arid or semi-arid habitats. The adaptive value of hard outer tunics is almost certainly that they provide protection to the bulb from excessively high summer temperatures.

Bulb apex (character 6)

The weighted consensus tree (Figure 50) suggests that extended bulb apices have evolved from non-extended bulb apices in numerous different areas and habitats, seven times (at node 205, *L. congesta* at node 212, *L. ameliae* at node 207, *L. zebrina* at node 188, *L. nordenstamii* at node 187, *L. arida* at node 151, and *L. giessii* at node 150), with three reversals. The trait occurs in southern Namibia, the Richtersveld, Namaqualand, western Bushmanland, the Roggeveld Plateau, the western and central Great Karoo, and the Little Karoo. With the exception of *L. dehoopensis* from the southern part of the Western Cape, species with extended bulb apices occur in arid habitats, and correlate to deeply embedded bulbs, providing protection from excessively high summer temperatures and desiccation.

Bulb apex outer tunics (character 7)

In the weighted consensus tree (Figure 50), non-fasciculate bulb apex outer tunics have evolved from fasciculate outer tunics twice (at nodes 276 and 190), with four reversals. Species with non-fasciculate outer tunics occur across the genus in geographically widely separated areas and habitats, whereas most species with fasciculate outer tunics are restricted to arid habitats, such as southern Namibia, Namaqualand, the Knersvlakte and the western

Great Karoo. The precise adaptive value of fasciculate bulb apex outer tunics is unknown.

Inner cataphyll apex shape (character 8)

In the weighted consensus tree (Figure 50), inner cataphylls with acute apices have evolved from those with obtuse apices in geographically widely separated areas and habitats. The switch has occurred on 16 occasions (at nodes 245, 206, 146, 154, *L. elegans* var. *elegans* at node 243, *L. violacea* at node 228, *L. leipoldtii* at node 226, *L. physocaulos* at node 225, *L. margaretae* at node 233, *L. youngii* at node 232, *L. unicolor* at node 217, *L. karooica* at node 143, *L. esterhuysenae* at node 170, *L. zeyheri* at node 159, *L. campanulata* at node 153, and *L. multifolia* at node 152), with three reversals. The trait occurs in Namaqualand, the Bokkeveld Plateau, the eastern Great Karoo, the Little Karoo, the western, southwestern and southern parts of the Western Cape, and in the Eastern Cape. A polymorphic condition has evolved from inner cataphylls with obtuse apices twice (at node 268 and *L. nervosa* at node 230). The adaptive value of inner cataphyll apex shape is unclear, and does not appear to correlate to current habitat.

Inner cataphyll adhesion to clasping leaf bases (character 9)

The weighted consensus tree (Figure 50) suggests that adherent inner cataphylls have evolved from non-adherent inner cataphylls in geographically widely separated taxa, in different habitats, and has arisen 14 times (at nodes 276, 219, 204, 195, 238, 232, *L. aloides* var. *aurea* at node 257, *L. pusilla* at node 252, *L. longibracteata* at node 242, *L. lutea* at node 249, *L. leipoldtii* at node 226, *L. rosea* at node 234, *L. youngii* at node 232, and *L. nutans* at node 175). The trait occurs in southern Namibia, Namaqualand, the Roggeveld Plateau, and the western, southwestern and southern parts of the Western Cape. In addition, the state has reversed on 19 separate occasions and is clearly under strong selective pressure. A polymorphic condition has evolved from non-adherent inner cataphylls in *L. bulbifera* (at node 258). The functional significance of the different inner cataphyll adhesion states is not

immediately apparent, and does not appear to correlate to habitat.

Leaf base markings (character 11)

The weighted consensus tree (Figure 50), indicated that convergence and reversal of immaculate, banded and spotted clasping leaf bases have occurred independently in widely separated areas, in different habitats. Banded leaf bases have evolved from immaculate leaf bases 10 times (at nodes 248, 223, 206, 188, 186, 165, 144, *L. marginata* subsp. *marginata* at node 255, *L. mediana* var. *rogersii* at node 237, and *L. dehoopensis* at node 192), with four reversals. The trait occurs in the Richtersveld, Namaqualand, the Bokkeveld Plateau, the western and central Great Karoo, and the western, southwestern and southern parts of the Western Cape.

Spotted leaf bases have evolved from immaculate leaf bases 10 times (at nodes 245, 242, 155, *L. aloides* var. *vanzyliae* at node 263, *L. rubida* at node 258, *L. violacea* at node 228, *L. variegata* at node 221, *L. leipoldtii* at node 226, *L. ameliae* at node 207, and *L. klinghardtiana* at node 173). The character state occurs in the Richtersveld, the western and southern parts of the Western Cape, and in the Little Karoo.

Spotted leaf bases have also evolved from banded leaf bases, on three occasions (*L. canaliculata* at node 200, *L. aurioliae* at node 143 and *L. latimerae* at node 181). Taxa with this character derivation occur in Namaqualand, the southern Great Karoo, the southeastern part of the Western Cape and in the Eastern Cape. Spotting and banding patterns are thought to assist in disrupting the outline of the shoot, thus effecting camouflage from herbivores during early growth phases.

Leaf number (character 12)

The weighted consensus tree (Figure 50) showed that similar leaf numbers have evolved on

numerous occasions in different areas and habitats. Solitary leaves have evolved from those that always have two leaves, six times (at nodes 190, 165, 146, *L. leomontana* at node 231, *L. convallarioides* at node 158, and *L. glaucophylla* at node 154), with one reversal. The trait occurs in the Richtersveld, Namaqualand, the Roggeveld Plateau, the western parts of the Western Cape, the western and central parts of the Great Karoo, and in the Eastern Cape.

Taxa with one or two leaves derived from species which are invariably two-leaved, nine times (at nodes 273, 258, 200, 192, 143, *L. esterhuysenae* at node 170, *L. zeyheri* at node 159, *L. comptonii* at node 154, and *L. namibiensis* at node 149), with six reversals. This character state is distributed from southern Namibia to the western and southern parts of the Western Cape to the Little Karoo and the southern parts of the Great Karoo. The evolution of taxa with one or two leaves from solitary leaved ancestors has only occurred twice (*L. latimerae* at node 181, and *L. xerophila* at node 173), with four reversals.

Taxa with three or more leaves have evolved from a range of basal states. They have evolved from those always having two leaves, four times (at nodes 163, *L. polyphylla* at node 148, *L. multifolia* at node 152, and *L. orthopetala* at node 161), and from solitary leaved ancestors, once (*L. moniliformis* at node 176), and from those with one or two leaves, once (at node 252). *P. corymbosa*, the only species with two or more leaves, has evolved from an ancestor with one or two leaves, once (at node 272).

Natural selection appears to act quickly in establishing the phyllotaxy of species, and leaf number has been modified quickly and continuously through time. In a number of species with relatively wide distributions such as *L. bulbifera*, *L. pustulata* and *L. rubida*, one or two leaves per individual occur within the same population. The character is truly polymorphic in these species as both states occur in all populations observed, and bears no correlation to maturity. The adaptive value of leaf number is unclear and does not appear to correlate to habitat.

Leaf orientation (character 13)

Spreading to suberect leaves occur across the entire distribution of *Lachenalia* and *Polyxena*, in numerous different habitats, and the weighted consensus tree (Figure 50) showed that they have evolved from prostrate leaves once (at node 276), with five reversals. Erect leaves have evolved from spreading to suberect leaves six times (at node 163, *L. haarlemensis* at node 181, *L. moniliformis* at node 176, *L. patula* at node 147, *L. polyphylla* at node 148, and *L. multifolia* at node 152). The trait occurs in the Knersvlakte, the western and southern parts of the Western Cape, and the Little Karoo. The functional significance of leaf orientation is unclear and does not appear to correlate to moisture or competition for light, as the different states occur in arid, semi-arid and relatively moist environments, as well as in exposed aspects and relatively dense vegetation.

Pustulate/non-pustulate adaxial leaf surface (character 14)

The weighted consensus tree (Figure 50) showed that pustulate adaxial leaf surfaces have evolved from non-pustulate surfaces on five occasions (at node 217, *L. stayneri* at node 230, *L. valeriae* at node 209, *L. minima* at node 199, and *L. liliiflora* at node 161). The trait occurs in Namaqualand, the Little Karoo, and the western and southwestern parts of the Western Cape. The polymorphic condition has evolved from non-pustulate surfaces three times (*L. nervosa* at node 230, *L. pustulata* at node 215, and *L. carnosa* at node 213). This trait occurs in Namaqualand, and the western and southern parts of the Western Cape. Polymorphic species display both states in all observed populations. The functional significance of pustules is unclear and does not appear to correlate to habitat.

Adaxial leaf trichomes (character 15)

In the weighted consensus tree (Figure 50), simple adaxial leaf trichomes have evolved from glabrous leaf surfaces twice (*L. ameliae* at node 207, and *L. comptonii* at node 154). Present

distribution of this character state is in the Little Karoo. Stellate adaxial leaf trichomes have evolved from glabrous leaf surfaces twice (at nodes 270 and 146). This trait occurs in the Richtersveld, Namaqualand, and the northwestern parts of the Western Cape. Trichomes are likely to have evolved under a whole regime of selective pressures for they form the interface between plant and the environment. Clearly they are involved in mitigating physical stresses such as cold, light and heat loading by insulating the mesophyll. They also reduce the flow of air across stomata and thus lower transpiration rates (Esau 1977). A number of researchers have also shown a link between indumentum and protection against insect predation, oviposition and nutrition of larvae (Levin 1973).

Adaxial leaf maculation (character 16)

The weighted consensus tree (Figure 50) showed that leaves that are always maculate have evolved repeatedly from immaculate ancestors. The character state occurs in numerous widely separated areas and in different habitats, and originated 13 times (at nodes 242, 203, 144, *L. pusilla* at node 252, *L. marginata* subsp. *neglecta* at node 248, *L. muirii* at node 243, *L. elegans* var. *membranacea* at node 244, *L. leomontana* at node 231, *L. nardouwensis* at node 219, *L. kliprandensis* at node 212, *L. obscura* at node 200, *L. undulata* subsp. *undulata* at node 197, and *L. contaminata* var. *contaminata* at node 163), with one reversal. The trait occurs in western Bushmanland, Namaqualand, the Bokkeveld Plateau, the western and southern parts of the Western Cape, and the southern parts of the Great Karoo.

Polymorphism with respect to maculation condition has evolved from immaculate ancestors on 14 occasions (at nodes 269, *L. fistulosa* at node 247, *L. violacea* at node 228, *L. salteri* at node 238, *L. rosea* at node 234, *L. margaretae* at node 233, *L. variegata* at node 221, *L. carnososa* at node 213, *L. verticillata* at node 206, *L. duncanii* at node 196, *L. doleritica* at node 194, *L. neilii* at node 141, *L. orthopetala* at node 161, and *L. campanulata* at node 153), with two reversals. This trait occurs in western Bushmanland, Namaqualand, the Bokkeveld Plateau, the western, southwestern and southern parts of the Western Cape, and in the Eastern

Cape. The polymorphic condition has been independently derived from a maculate ancestor once (*L. bulbifera* at node 258). Polymorphism has stabilised into a single state, four times. Like leaf base markings, the adaptive value of maculate adaxial leaf surfaces is thought to assist in herbivore avoidance by confusing search images through camouflage.

Leaf shape (character 17)

Leaf shape varies greatly in *Lachenalia* but is relatively fixed within species. The weighted consensus tree (Figure 50) suggests that similar leaf shapes have evolved convergently on numerous independent occasions, and reversals are also common. Lanceolate leaves occur across the genus in different areas and habitats, and have evolved from ovate leaves twice (at nodes 275 and 269), with seven reversals.

Linear leaves have evolved from ovate leaves twice (*P. paucifolia* at node 273, and *P. corymbosa* at node 272), and occur in species from the western and southwestern parts of the Western Cape.

Linear leaves have also evolved from lanceolate leaves on five occasions (at node 180, *L. barkeriana* at node 252, *L. youngii* at node 232, *L. namaquensis* at node 207, and *L. dehoopensis* at node 192), with eight reversals. This trait occurs in Namaqualand, the Roggeveld Plateau, and the western and southern parts of the Western Cape. Although it might be expected that linear leaves are a modification to arid environments, and that ovate leaves are an adaptation to competing for light and are a modification to moister habitats, there appears to be no correlation between leaf shape and habitat; linear leaves have evolved in both moist and arid habitats (e.g. *L. contaminata*, *L. barkeriana* respectively) and the same is true of ovate leaves (e.g. *L. bulbifera*, *L. kliprandensis* respectively). However our perception of phylogeny and evolution is limited to one point in time, and characters evolved under different environmental conditions may persist if they do not impinge heavily upon organism fitness.

Distal lamina profile (character 18)

In the weighted consensus tree (figure 50), canaliculate distal lamina profile has evolved from flat distal lamina profile independently 14 times, in numerous different areas and habitats (at nodes 268, 238, 206, *P. longituba* at node 275, *P. paucifolia* at node 273, *P. corymbosa* at node 272, *L. algoensis* at node 264, *L. rubida* at node 258, *L. arbutnotiae* at node 242, *L. murii* at node 243, *L. rosea* at node 234, *L. youngii* at node 232, *L. framesii* at node 210, and *L. karooica* at node 143), with 10 reversals. The trait occurs in the western, southwestern and southern parts of the Western Cape, and in the Knersvlakte and the Great Karoo.

Convex distal laminae have evolved from flat laminae once (*L. namaquensis* at node 207), with one reversal, and from canaliculate laminae mainly in the western and southern parts of the Western Cape, and also in the Knersvlakte and the western Great Karoo. Such leaves have evolved seven times (at nodes 171, 163, 148, *L. moniliformis* at node 176, *L. mathewsii* at node 166, *L. multifolia* at node 152, and *L. zeyheri* at node 159). The adaptive value of distal lamina profile is unclear.

Basal lamina profile (character 19)

Canaliculate bases occur across the entire distribution of *Lachenalia* in numerous different habitats, and the weighted consensus tree (Figure 50) showed that this state has evolved from flat basal lamina profile twice (at node 273, and *P. longituba* at node 275), with 13 reversals. The adaptive value of basal lamina profile is unclear and does not appear to correlate to habitat.

Adaxial leaf tertiary sculpturing (character 20)

The weighted consensus tree (Figure 50), suggests that similar adaxial leaf tertiary sculpturing states have evolved convergently on many occasions, and reversals are also common. The

character yields no useful phylogenetic information.

Abaxial leaf tertiary sculpturing (character 21)

In the weighted consensus tree (Figure 50), abaxial sculpturing is highly mutable and provides no useful phylogenetic pattern.

Leaf margin anatomy (character 22)

The weighted consensus tree (Figure 50) showed that flabellate margins have evolved from simple margins in numerous different areas and in different habitats, on three occasions (at nodes 269 and 204, and *L. klinghardtiana* at node 173), with six reversals. The trait occurs in the Richtersveld, Namaqualand, western Bushmanland, the Bokkeveld Plateau, and the western, southwestern and southern parts of the Western Cape.

'Polyxena' margins have evolved from simple margins seven times (at nodes 274, 162 and 153, *L. namaquensis* at node 207, *L. attenuata* at node 179, *L. arida* at node 151, and *L. giessii* at node 150), with one reversal. This trait occurs in southern Namibia, Namaqualand, the Bokkeveld Plateau, the Roggeveld Plateau and the Eastern Cape. 'Polyxena' margins have also evolved from flabellate margins, six times (at nodes 258, 197, 141, *L. congesta* at node 212, *L. isopetala* at node 194, and *L. komsbergensis* at node 183), with one reversal. The character state occurs in Namaqualand, the Bokkeveld Plateau, the Roggeveld Plateau, and the western, southwestern and southern parts of the Western Cape.

Multiple epidermal margins have evolved from simple margins once (*L. verticillata* at node 206), and from flabellate margins once (*L. stayneri* at node 230). Sclerotic margins have evolved from flabellate margins twice (*L. nervosa* at node 230 and *L. duncanii* at node 196). The adaptive value of sclerotic leaf margins is thought to be linked to protection against edge-feeding insects.

Leaf margin shape (character 23)

In the weighted consensus tree (Figure 50), crisped margins have evolved from flat margins in numerous different areas and habitats, 18 times (at nodes 248, 223, 173, *L. reflexa* at node 268, *L. marginata* subsp. *marginata* at node 255, *L. violacea* at node 228, *L. ventricosa* at node 224, *L. mediana* var. *rogersii* at node 237, *L. variegata* at node 221, *L. framesii* at node 210, *L. verticillata* at node 206, *L. undulata* subsp. *undulata* at node 197, *L. duncanii* at node 196, *L. isopetala* at node 194, *L. zebrina* at node 188, *L. buchbergensis* at node 187, *L. wieseii* at node 186, and *L. komsbergensis* at node 183). The character state occurs in the Richtersveld, Namaqualand, western Bushmanland, the Knersvlakte, the Roggeveld Plateau, the western and central parts of the Great Karoo, and the western and southwestern parts of the Western Cape. The adaptive value of the crisped margin state is not immediately apparent although crisped margins occur primarily in arid habitats.

Leaf margin vesture (character 24)

In the weighted consensus tree (Figure 50), ciliolate margins have evolved from glabrous margins twice (at node 275 and *L. polyphylla* at node 148). Ciliate margins have evolved from glabrous ancestors three times (at node 178, *L. ameliae* at node 207, and *L. comptonii* at node 154), and stellate margins have evolved from glabrous margins twice (at nodes 270 and 146). The functional significance of ciliolate, ciliate and stellate margin vesture could be linked to protection against edge-feeding insects.

Leaf apex shape (character 25)

The weighted consensus tree (Figure 50) showed that acute leaf apices have evolved from naviculate apices in numerous different areas and habitats, six times (at node 177, *P. longituba* at node 275, *P. paucifolia* at node 273, *P. corymbosa* at node 272, *L. youngii* at node 232, and *L. namaquensis* at node 207), with six reversals. The trait occurs in Namaqualand, the

Knersvlakte, the Roggeveld Plateau, the Little Karoo, the western, southwestern and southern parts of the Western Cape, and in the Eastern Cape. The functional significance of naviculate and acute leaf apex shape is unclear.

Primary seedling leaf orientation and shape (characters 26 and 27)

The weighted consensus tree (Figure 50), showed that the different primary seedling leaf orientations and seedling leaf shapes (prostrate, suberect and erect; flat and terete) have evolved repeatedly.

Erect, terete seedling leaves evolved from a prostrate, flat leaved ancestor seven times (at nodes 275, 268, 256, 211, *L. aloides* var. *thunbergii* at node 262, *L. bulbifera* at node 258, and *L. youngii* at node 232). The trait occurs in southern Namibia, Namaqualand, western Bushmanland, the Knersvlakte, the Bokkeveld Plateau, the Little Karoo, the western, southwestern and southern parts of the Western Cape, and in the Eastern Cape.

Erect, terete seedling leaves have evolved from the suberect seedling leaf trait once (*L. mutabilis* at node 224), with four reversals.

The adaptive value of seedling leaf orientation and shape is not clear, although the brownish colouring of prostrate seedling leaves does provide excellent camouflage. It would be expected that erect seedling leaves would correlate to arid, exposed habitats where abundant light is available and heat loading is a factor. In such habitats transpiration could be reduced by reduced leaf areas, but this state occurs across the genus, irrespective of habitat or degree of aridity. Similarly, species with prostrate, expanded blades might be suspected to be an adaptation to competition for light, are not restricted to moister habitats.

10.2.3.2 Reproductive homoplasy

Peduncle elevation at anthesis (character 28)

In the weighted consensus tree (Figure 50), aerial peduncles have evolved from subterranean peduncles once (at node 273), with two reversals. The functional significance of aerial peduncles is thought to be strongly linked to anemochory; the peduncles of species that are subterranean at anthesis, elongate during the fruiting stage to facilitate anemochory.

Peduncle inflation (character 29)

The weighted consensus tree (Figure 50) showed that inflated peduncles have evolved from non-inflated peduncles four times (at nodes 228, 224, 175, and *L. barkeriana* at node 252). The trait occurs in southern Namibia, the Richtersveld, Namaqualand, western Bushmanland, and the northwestern, western and southwestern parts of the Western Cape. The polymorphic condition has evolved from inflated peduncles once (*L. mutabilis* at node 224). Inflated peduncles occur mainly in arid habitats but their adaptive value is not immediately apparent.

Rachis apical anthocyanins (character 30)

In the weighted consensus tree (Figure 50), rachis apical anthocyanins have evolved from those devoid of apical anthocyanins once (at node 273), and seven reversals occur. The colourful anthocyanin colours are thought to be linked to pollinator attraction.

Rachis apical carotenoids (character 31)

In the weighted consensus tree (Figure 50), rachis apical carotenoids have evolved from those devoid of apical carotenoids twice (at node 262, and *L. arbutnotiae* at node 242), with

one reversal. Like rachis apical anthocyanins, rachis apical carotenoids are presumed to be linked to pollinator attraction.

Rachis apical chlorophylls (character 32)

The weighted consensus tree (Figure 50) showed that rachis apical chlorophylls have evolved from those devoid of apical chlorophylls twice (at node 197, and *L. bowkeri* at node 192). The adaptive value of rachis apical chlorophylls is unclear.

Rachis apex structural white (character 33)

In the weighted consensus tree (Figure 50), the absence of rachis apex structural white has evolved from rachis structural white once (at node 273), with three reversals. The functional significance of rachis apex structural white is unclear, and does not appear to correlate to habitat.

Upper bract shape (character 35)

In the weighted consensus tree (Figure 50), ovate upper bracts have evolved from lanceolate bracts 16 times (at nodes 270, 258, 252, 228, 207, 200, 186, *L. muirii* at node 243, *L. bolusii* at node 223, *L. purpureocaerulea* at node 217, *L. fasciculata* at node 203, *L. isopetala* at node 194, *L. alba* at node 142, *L. neilii* at node 141, *L. aurioliae* at 143, and *L. zebrina* at node 188), with five reversals. The trait occurs in the Richtersveld, Namaqualand, the Bokkeveld Plateau, the Roggeveld Plateau, the western and central Great Karoo, the Little Karoo, and the northwestern, western, southwestern and southern parts of the Western Cape. The evolution of cup-shaped upper bracts from ovate upper bracts has occurred once (at node 164). The adaptive value of upper bract shape traits could form part of pollinator attraction.

Inflorescence type (character 36)

In the weighted consensus tree (Figure 50), spikes have evolved from racemes six times (at nodes 265, 250, 214, 224, *L. trichophylla* subsp. *trichophylla* at node 270, and *L. marginata* subsp. *marginata* at node 255), with one reversal. The trait occurs in Namaqualand, the Bokkeveld Plateau, the Roggeveld Plateau, and the western, southwestern, and southern parts of the Western Cape. A polymorphic condition has evolved from racemes twice (*L. capensis* at node 254, and *L. karooica* at node 143), and from spikes three times (*L. longibracteata* at node 242, *L. marlothii* at node 248, and *L. obscura* at node 200). The adaptive value of the different inflorescence types could be linked to pollinator attraction and support.

Pedicel orientation at anthesis (character 37)

In the weighted consensus tree (Figure 50) suberect pedicels have evolved from erect pedicels twice (at node 268, and *L. trichophylla* subsp. *massonii* at node 270). The trait occurs in Namaqualand and in the western and southwestern parts of the Western Cape. The loss of pedicels from erect pedicels has occurred twice (at node 267 and *L. trichophylla* subsp. *trichophylla* at node 270), with one reversal. This trait occurs on the Bokkeveld Plateau, and in the northwestern, western, southwestern and southern parts of the Western Cape. Spikes have been derived from suberect pedicels twice (at nodes 224 and 214), with one reversal, and the trait occurs in Namaqualand, the Roggeveld Plateau, the Knersvlakte and the Little Karoo. Pedicels that are curved downwards have evolved from suberect pedicels twice (at node 168 and *L. nordenstamii* at node 187). This trait occurs in the Richtersveld and in the southern parts of the Western Cape. Patent pedicels have evolved from suberect pedicels three times (at nodes 146 and 170, and *L. wiesei* at node 186), and this trait occurs in the Richtersveld, Namaqualand, and the northwestern, western and southern parts of the Western Cape. Like inflorescence type, the functional significance of pedicel orientation at anthesis could be linked to pollinator attraction and support.

Perianth shape (character 38)

In the weighted consensus tree (Figure 50), oblong-campanulate perianths have evolved from tubular perianths once (at node 251), with five reversals. Narrowly campanulate perianths have evolved from oblong-campanulate perianths three times (at nodes 164, *L. anguinea* at node 175, and *L. juncifolia* var. *campanulata* at node 170). The trait occurs in Namaqualand, the western, southwestern and southern parts of the Western Cape, and in the Eastern Cape. Widely campanulate perianths have evolved from oblong-campanulate perianths twice (*L. nervosa* at node 230, and *L. nordenstamii* at node 187), with one reversal, and from narrowly campanulate perianths once (at node 157). Urceolate perianths have evolved repeatedly from oblong-campanulate perianths, eight times (at nodes 247, 213, 210, *L. bolusii* at node 223, *L. mutabilis* at node 224, *L. peersii* at node 234, *L. urceolata* at node 201, and *L. aurioliae* at node 143), with one reversal. This trait occurs in Namaqualand, the Knersvlakte, the Roggeveld Plateau, the Bokkeveld Plateau, the northwestern, southwestern and southern parts of the Western Cape, and in the Little Karoo. The functional significance of the different perianth shapes is strongly linked to breeding systems.

Flower arrangement (character 41)

In the weighted consensus tree (Figure 50), flowers in whorls of three flowers have evolved from spirally arranged flowers six times (at nodes 245, 206, *L. trichophylla* subsp. *trichophylla* at node 270, *L. marlothii* at node 248, *L. aurioliae* at node 143, and *L. wiesei* at node 186), with one reversal. The trait occurs in Namaqualand, the Bokkeveld Plateau, the northwestern parts of the Western Cape, and the southern Great Karoo. The adaptive value of the different flower arrangement states is unclear, but may be linked to pollinator attraction.

Outer tepal shape (character 42)

In the weighted consensus tree (Figure 50), ovate outer tepal shape has evolved from oblong

outer tepal shape twice (at nodes 255 and 265), with four reversals. Oblong and ovate outer tepal shape are thought to form part of pollinator attraction.

Outer tepal length (character 43)

In the weighted consensus tree (Figure 50), long outer tepals have evolved from short outer tepals three times (at node 264, *L. isopetala* at node 194, and *L. sargeantii* at node 168). Present distribution of this character state is on the Roggeveld Plateau, the western Great Karoo, the western, southwestern and southern parts of the Western Cape, and in the Eastern Cape. Long outer tepals are thought to be linked to the sunbird pollination syndrome in certain species.

Outer tepal apex (character 44)

The weighted consensus tree (Figure 50) indicated that flat outer tepal apices have evolved from recurved tepal apices once (at node 271), with nine reversals. The adaptive value of flat and recurved outer tepal apices may correlate to pollinator syndromes.

Inner tepal shape (character 45)

In the weighted consensus tree (Figure 50), obovate inner tepals have evolved from linear-oblong inner tepals once (at node 271), with seven reversals. Oblong-obovate inner tepals have evolved from obovate inner tepals twice (at node 266, and *L. sargeantii* at node 168). This trait occurs in the northwestern, western, southwestern and southern parts of the Western Cape. Like long outer tepals, oblong-obovate inner tepals are thought to be linked to the sunbird pollination syndrome.

Inner tepal length (character 46)

In the weighted consensus tree (Figure 50), long inner tepals have evolved from short inner tepals twice (at node 266, and *L. sargeantii* at node 168). The trait occurs in the northwestern, western, southwestern and southern parts of the Western Cape. Like long outer tepals and oblong-obovate inner tepal shape, long inner tepals are thought to be linked to sunbird pollination.

Inner and outer tepal arrangement (character 47)

In the weighted consensus tree (Figure 50) inner tepals that are longer than the outer tepals have evolved from subequal inner and outer tepals nine times (at nodes 271, 173, 168, 165, 161, *L. leomontana* at node 231, *L. bachmannii* at node 160, *L. patula* at node 147, and *L. polypodantha* at node 146), with 12 reversals. The trait occurs in numerous geographically widely separated areas including the Richtersveld, Namaqualand, the Knersvlakte, western Bushmanland, and the western, southwestern and southern parts of the Western Cape. The adaptive value of the different inner and outer tepal arrangements is not immediately apparent, but may be linked to pollinator attraction.

Floral symmetry (character 48)

The weighted consensus tree (Figure 50) showed that zygomorphic floral symmetry evolved from actinomorphic floral symmetry once (at node 271), and one reversal occurs. The functional significance of floral symmetry is almost certainly linked to pollinator behaviour.

Ventral inner tepal extension (character 49)

In the weighted consensus tree (Figure 50), inner tepals in which the ventral tepal is shorter than the upper two tepals, have evolved from inner tepals that are all equal, four times (at

nodes 268, 258, *L. capensis* at node 254, and *L. martiniae* at node 223). The trait occurs in the northwestern, western, southwestern and southern parts of the Western Cape. Elongation of the lower inner tepal in relation to its upper correlates has evolved repeatedly from equal inner tepals in numerous widely separated areas and habitats. The switch has occurred 16 times (at nodes 270, 248, 238, 216, 179, 166, 142, *L. marginata* subsp. *marginata* at node 255, *L. bolusii* at node 223, *L. mutabilis* at node 224, *L. thomasiae* at node 220, *L. canaliculata* at node 200, *L. doleritica* at node 194, *L. maximiliani* at node 189, *L. perryae* at node 185, and *L. klinghardtiana* at node 173), with two reversals. This trait occurs in the Richtersveld, Namaqualand, the Bokkeveld Plateau, the northwestern, western, southwestern and southern parts of the Western Cape, and on the Roggeveld Plateau. The adaptive value of a longer lower inner tepal is almost certainly specialisation for bee pollination in certain species with oblong-campanulate and urceolate flowers, providing the insect with a landing platform from which to enter the flower.

Filament orientation at anthesis (character 50)

In the weighted consensus tree (Figure 50), narrowly spreading filaments have evolved from straight filaments twice (at node 161, and *L. nordenstamii* at node 187). The trait occurs in the Richtersveld and in the southwestern parts of the Western Cape. Recurved filaments have evolved from straight filaments in numerous widely separated areas and habitats, six times (at nodes 142, 157, *P. ensifolia* at node 274, *L. muirii* at node 243, *L. nervosa* at node 230, and *L. karooica* at node 143). The trait occurs in Namaqualand, the Bokkeveld Plateau, the western and southern parts of the Western Cape, the Little Karoo, the central and eastern Great Karoo, and in the Eastern Cape. Declinate filaments have evolved from straight filaments in numerous different areas and habitats, eight times (at nodes 237, 226, 176, *L. canaliculata* at node 200, *L. duncanii* at node 196, *L. aurioliae* at node 143, *L. whitehillensis* at node 184, and *L. mathewsii* at node 166), with three reversals. This trait occurs in the Richtersveld, Namaqualand, western Bushmanland, the northwestern and western parts of the Western Cape, the southern Great Karoo, and in the Little Karoo. Declinate filaments have also

evolved from recurved filaments twice (at node 147, and *L. dasybotrya* at node 141). The trait occurs in the Richtersveld, Namaqualand, the Knersvlakte, and in the western Great Karoo. The functional significance of the different filament orientation states at anthesis is thought to correlate to pollination syndromes.

Filament colour (character 51)

In the weighted consensus tree (Figure 50), filaments that are white in the lower half and purple or magenta in the upper half have evolved from white filaments in numerous widely separated areas and habitats on 10 occasions (*L. violacea* at node 228, *L. physocaulos* at node 225, *L. purpureocaerulea* at node 217, *L. splendida* at node 211, *L. duncanii* at node 196, *L. nordenstamii* at node 187, *L. haarlemensis* at node 182, *L. polypodantha* at node 146, *L. macgregoriorum* at node 153, and *L. comptonii* at node 154). The trait occurs in the Richtersveld, Namaqualand, the Knersvlakte, western Bushmanland, the Little Karoo, the Bokkeveld Plateau, and the western and southern parts of the Western Cape. A polymorphic condition has evolved from white filaments once (*P. ensifolia* at node 274). All taxa displaying the derived condition have filaments that are well exerted beyond the perianth and are almost certainly linked to pollinator attraction.

Filament relative lengths (character 53)

In the weighted consensus tree (Figure 50), subequal inner and outer filaments have evolved from equal inner and outer filaments twice (at nodes 276 and 148), with two reversals. The functional significance of equal and subequal filaments may correlate to pollination syndromes.

Outer filament insertion (character 54)

In the weighted consensus tree (Figure 50), medial outer filament insertion has evolved from

upper outer filament insertion once (at node 272), with one reversal. Basal outer filament insertion has evolved from medial outer filament insertion once (at node 263). The different outer filament insertion positions may correlate to pollination syndromes.

Pollen exine sculpturing (character 56)

In the weighted consensus tree (Figure 50), reticulate pollen exine sculpturing has evolved from rugose exine sculpturing twice (at node 269, and *L. polypodantha* at node 146), with 10 reversals. The adaptive value of the different pollen exine sculpturing states is unclear.

Style orientation at anthesis (character 57)

The weighted consensus tree (Figure 50), indicated that declinate styles have evolved from straight styles in numerous widely separated areas and habitats on 10 occasions (at nodes 237, 226, 176, 147, *L. canaliculata* at node 200, *L. duncanii* at node 196, *L. whitehillensis* at node 184, *L. mathewsii* at node 166, *L. dasybotrya* at node 141, and *L. aurioliae* at node 143), with three reversals. The trait occurs in the Richtersveld, Namaqualand, western Bushmanland, the western and southern Great Karoo, the Little Karoo, and in the western and southwestern parts of the Western Cape. Declinate style orientation has evolved largely in conjunction with declinate filament orientation and is thought to correlate to pollination syndromes.

Ovary shape (character 58)

The weighted consensus tree (Figure 50), suggested that ellipsoid ovaries have evolved from obovoid ovaries in numerous widely separated areas and habitats. This switch in ovary shape has occurred on six occasions (at nodes 275, 271, 167, *L. klinghardtiana* at node 173, *L. comptonii* at node 154, and *L. patula* at node 147), with six reversals. The trait occurs in the Richtersveld, Namaqualand, the Knersvlakte, the Roggeveld Plateau, the Little Karoo, the southern parts of the Western Cape, and in the western and southern Great Karoo. The

functional significance of the different ovary shape states is unclear but may be linked to seed dispersal mechanisms.

Capsule shape (character 59)

In the weighted consensus tree (Figure 50), ellipsoid capsules have evolved from obovoid capsules in widely separated areas and habitats on five occasions (at nodes 271, 167, *L. klinghardtiana* at node 173, *L. comptonii* at node 154 and *L. patula* at node 147), with five reversals. The character state occurs in the Richtersveld, Namaqualand, the Knersvlakte, the western and southwestern parts of the Western Cape, and in the Little Karoo. Ovoid capsules have evolved from obovoid capsules once (at node 275), and obcordate capsules have evolved from ellipsoid capsules once (at node 188). The functional significance of the different capsule shape states is almost certainly linked to seed dispersal, of which the obcordate, broadly winged capsules of three species (*L. buchbergensis*, *L. nordenstamii* and *L. zebrina*) are wind dispersed (anemochory).

Capsule orientation (character 60)

In the weighted consensus tree (Figure 50), capsules that bend upwards have evolved from those that retain the same orientation as their flowers, seven times (at nodes 263, 178, 169, *L. purpureocaerulea* at node 217, *L. pustulata* at node 215, *L. polyphylla* at node 148, and *L. polypodantha* at node 146), with five reversals. The trait occurs in the Richtersveld, Namaqualand, and the western and southwestern parts of the Western Cape. Capsules that bend downwards have evolved from those that retain the same orientation as their flowers, once (*L. multifolia* at node 152). The adaptive value of the different capsule orientation states is almost certainly linked to seed dispersal mechanisms.

Capsule length (character 61)

In the weighted consensus tree (Figure 50), long capsules have evolved from short capsules on two occasions (at nodes 268 and 260). The trait only occurs in the western and southwestern parts of the Western Cape. The functional significance of the different capsule length states almost certainly forms part of seed dispersal strategy.

Infructescence (peduncle) elongation (character 62)

In the weighted consensus tree (Figure 50), non-elongated infructescences have evolved from elongated infructescences once (at node 271), with two reversals. The adaptive value of peduncle elongation is that it results in the infructescence being pushed upwards, causing it to fall over into a horizontal position a short distance away from the plant, allowing dispersal of seeds over a wider area.

Testa lustre (character 63)

In the weighted consensus tree (Figure 50), the evolution of seeds with matte black testas from those with glossy black testas has occurred in numerous widely separated areas and habitats, on ten occasions (at nodes 273, 206, 197, 193, 179, 168, 148, *L. bolusii* at node 223, *L. ameliae* at node 207, and *L. macgregoriorum* at node 153), with six reversals. The trait occurs in the Richtersveld, Namaqualand, the Knersvlakte, the Bokkeveld Plateau, the Little Karoo, the southern Great Karoo, and the western, southwestern and southern parts of the Western Cape. The functional significance of testa lustre is unclear. It does not correspond to strophiole length and thus does not appear to be linked to myrmecochory.

Seed length (character 64)

In the weighted consensus tree (Figure 50), short seeds have evolved from medium-length

seeds four times (at node 270, *L. muirii* at node 243, *L. patula* at node 147, and *L. angelica* at node 146). The trait occurs in Namaqualand, the Knersvlakte, and the northwestern, western and southern parts of the Western Cape. Long seeds have evolved from medium-length seeds six times (at nodes 194, 188, *L. congesta* at node 212, *L. xerophila* at node 173, *L. pearsonii* at node 149 and *L. schelpei* at node 144). This trait occurs in southern Namibia, the Richtersveld, Namaqualand, western Bushmanland, the Roggeveld Plateau, and the western and central Great Karoo. Long seeds have evolved exclusively in arid areas but the functional significance of the different seed length states is unclear.

Seed width (character 65)

In the weighted consensus tree (Figure 50), narrow seeds have evolved from medium-length seeds three times (at nodes 270, 148, and *L. muirii* at node 243), with one reversal. The trait occurs in Namaqualand, the Knersvlakte, and the northwestern, southwestern and southern parts of the Western Cape. Wide seeds have evolved from medium-width seeds seven times (at nodes 194, 151, *L. marlothii* at node 248, *L. congesta* at node 212, *L. zebrina* at node 188, *L. anguinea* at node 175, and *L. neilii* at node 141), with one reversal. The trait occurs in southern Namibia, Namaqualand, the Bokkeveld Plateau, the western and central Great Karoo, and on the Roggeveld Plateau. The functional significance of the different seed width states is not immediately apparent, but like long seeds, wide seeds appear to have evolved exclusively in arid areas.

Seed shape (character 66)

In the weighted consensus tree (Figure 50), ovoid seeds have evolved from globose seeds in numerous widely separated areas and habitats. This switch in seed shape has occurred on nine occasions (at nodes 275, 214, 161, *P. corymbosa* at node 272, *L. marlothii* at node 248, *L. ventricosa* at node 224, *L. attenuata* at node 179, *L. mathewsii* at node 166 and *L. glaucophylla* at node 154), with five reversals. The trait occurs in Namaqualand, the

Roggeveld Plateau, the western, southwestern and southern parts of the Western Cape, and in the Eastern Cape. Oblong seeds have evolved from globose seeds once (*L. xerophila* at node 173), and from ovoid seeds once (at node 187). The adaptive value of the different seed shape states is unclear.

Testa primary sculpturing (character 67)

The weighted consensus tree (Figure 50), suggested that rugose testa primary sculpturing has evolved from smooth testa primary sculpturing seven times (*P. corymbosa* at node 272, *L. bolusii* at node 223, *L. buchbergensis* at node 187, *L. wiesei* at node 186, *L. komsbergensis* at node 183, *L. polyphylla* at node 148, and *L. patula* at node 147). The trait occurs in the Richtersveld, Namaqualand, the Knersvlakte, the Roggeveld Plateau, and the northwestern and southwestern part of the Western Cape. The adaptive value of testa primary sculpturing traits are unknown.

Testa secondary sculpturing (character 68)

In the weighted consensus tree (Figure 50), reticulate secondary sculpturing has evolved from testas devoid of secondary sculpturing in numerous widely separated areas and habitats, 10 times (at nodes 270, 192, 178, 146, *L. glauca* at node 228, *L. framesii* at node 210, *L. namaquensis* at node 207, *L. inconspicua* at node 203, *L. perryae* at node 185, and *L. karooica* at node 143). The trait occurs in the Richtersveld, Namaqualand, the Kamiesberg, the Knersvlakte, the Little Karoo, the eastern parts of the Great Karoo, the western and southern parts of the Western Cape, and in the Eastern Cape. Colliculate secondary sculpturing has evolved from testas devoid of secondary sculpturing once (at node 168). Like testa primary sculpturing, the adaptive value of testa secondary sculpturing is unknown.

Strophiole length (character 69)

In the weighted consensus tree (Figure 50), medium-length strophioles have evolved from rudimentary strophioles in widely separated areas and habitats. The character state change occurred five times (at nodes 269, 208, *L. kliprandensis* at node 212, *L. klinghardtiana* at node 173, and *L. glaucophylla* at node 154), with three reversals. The trait occurs in the Richtersveld, Namaqualand, the Knersvlakte, the western, southwestern and southern parts of the Western Cape, the Roggeveld Plateau, and the Little Karoo. Long strophioles have evolved from rudimentary strophioles once (*L. attenuata* at node 179). Long strophioles have also evolved from medium-length strophioles, seven times (at nodes 264, 237, 144, *L. marlothii* at node 248, *L. variegata* at node 221, *L. inconspicua* at node 203, and *L. doleritica* at node 194), with one reversal. This trait occurs in Namaqualand, the western, eastern and southern parts of the Great Karoo, and the western and southwestern parts of the Western Cape. The functional significance of medium-length and long strophioles may be linked to myrmecochory. This method of dispersal has been observed in the field by Nordenstam (Müller-Doblies *et al.* 1987).

Strophiole texture (character 70)

In the weighted consensus tree (Figure 50), smooth strophioles have evolved from ridged strophioles once (at node 269), with two reversals. The adaptive value of the different strophiole texture states is unknown.

Strophiole inflation (character 71)

In the weighted consensus tree (Figure 50), inflated strophioles have evolved from non-inflated strophioles once (at node 269), with one reversal. The functional significance of inflated strophioles is unclear, but may be linked to myrmecochory that has been observed in *L. barkeriana* by Nordenstam (Müller-Doblies *et al.* 1987).

Raphe inflation (character 72)

In the weighted consensus tree (Figure 50), inflated raphes have evolved from non-inflated raphes twice (at node 258, and *L. xerophila* at node 173). At present this trait occurs in deep sandy habitats in Namaqualand, western Bushmanland, and the western, southwestern and southern parts of the Western Cape. Its functional significance is unclear.

Chalazal collar length (character 73)

In the weighted consensus tree (Figure 50), short chalazal collars have evolved from seeds without collars in numerous widely separated areas and habitats. The character state change occurred 11 times (at nodes 270, 252, 224, 210, *L. rubida* at node 258, *L. bolusii* at node 223, *L. carnososa* at node 213, *L. zebrina* at node 188, *L. perryae* at node 185, *L. glaucophylla* at node 154, and *L. patula* at node 147), with three reversals. The trait occurs in the Richtersveld, Namaqualand, the Knersvlakte, the western and central Great Karoo, the Roggeveld Plateau, and the northwestern, western, southwestern and southern parts of the Western Cape. Long chalazal collars have evolved from seeds without collars once (at node 187), and this trait currently only occurs in the Richtersveld and in southern Namibia. The adaptive value of the different chalazal collar traits is unclear.

Most character states appear to have evolved repeatedly and independently across *Lachenalia*; this can be ascribed to their high fitness value in providing expedient solutions to evolutionary problems. There is no doubt that the levels of homoplasy are not artificial constructs but that they represent convergent responses in a rapidly radiating genus. This situation is an expected one because the common phyletic base poses restrictions on the possible morphological answers to environmental challenges.

With regard to vegetative characters, a clear pattern that emerges is the convergent reversal

of certain character states in response to aridity: certain species from arid or semi-arid regions with solitary bulbs (character 4, state 0) and hard outer bulb tunics (character 5, state 0) such as *L. dasybotrya* from the western Great Karoo (at node 141), *L. martinae* from the Olifants River Mountains in the Western Cape (at node 223), and three species from southern Namibia, *L. arida*, *L. giessii* and *L. pearsonii* (at node 151), have evolved in tandem. Similarly, fasciculate bulb apex outer tunics (character 7, state 0) have evolved in tandem with solitary bulbs and hard outer bulb tunics in all the above-mentioned species, as well as in *L. namibiensis* (at node 151) from southern Namibia, and hard outer bulb tunics (character 5, state 0) and fasciculate bulb apex outer tunics (character 7, state 0), have evolved in tandem in *L. patula* from the Knersvlakte (at node 147). Extended bulb apices (character 6, state 1), another adaptation to aridity, have evolved in tandem with solitary bulbs in *L. congesta* from the Roggeveld Plateau (at node 212), *L. ameliae* from the Little Karoo (at node 207), *L. zebrina* from the western and central Great Karoo (at node 188), and *L. nordenstamii* from the Richtersveld (at node 187).

With regard to reproductive characters, a clear pattern that emerges is the convergent evolution of character states in response to sunbird pollination: basal outer filament insertion (at node 263, character 54, state 2) that includes all *L. aloides* taxa, *L. bulbifera* and *L. rubida*; long outer tepals (at node 264, character 43, state 1) that includes *L. algoensis*, all *L. aloides* taxa, *L. bulbifera* and *L. rubida*; oblong-obovate inner tepal shape (at node 266, character 45, state 2), and long inner tepals (at node 266, character 46, state 1), of which both of the latter states include *L. algoensis*, all *L. aloides* taxa, *L. bulbifera* and *L. rubida*. These states form part of a suite of character states in response to sunbird pollination that also include tubular perianth shape (character 38, state 0), long, tubular perianth tubes (character 39, state 0, and character 40, state 0, respectively), and oblong outer tepal shape (character 42, state 0). The *L. orchioides* taxa (at node 265) resolve as sister taxa in the basal part of the 'sunbird-pollinated' clade (at node 266) and are supported by some of the convergent character states associated with sunbird pollination, but are not considered to be sunbird-pollinated by virtue

of their short outer tepals and heavily sweet-scented flowers. The sunbird-pollinated sister species *L. reflexa* and *L. viridiflora* (at node 268) do not resolve as part of the ‘sunbird-pollinated’ clade, but are placed on a branch of their own immediately below the ‘sunbird-pollinated’ clade.

Perianth shape is stable within species but appears to be a highly malleable character, becoming highly specialised in certain species (like *L. aloides* and *L. bulbifera*) with brightly coloured flowers for attracting sunbird pollinators. Two of the sunbird-pollinated species (*L. bulbifera* and *L. rubida*) have relatively wide distribution ranges extending along the coast of the northwestern, western, southwestern and southern parts of the Western Cape. The distribution of *L. aloides* including all its varieties is similar but extends further inland in the Western Cape. *L. viridiflora* has a highly restricted distribution on the west coast of the Western Cape, and the variable *L. reflexa* is widespread in the western and southwestern parts of the Western Cape, while the putatively sunbird-pollinated *L. algoensis* occurs along the south coast of the Western Cape and in the Eastern Cape.

Most *Lachenalia* species are bee-pollinated and share the same suites of convergent character states including oblong- campanulate, narrowly campanulate, widely campanulate or urceolate perianth shapes, short, ovate outer tepals, and short, linear-oblong or obovate inner tepal shape.

Because reproductive characters are tightly constrained by the morphology of pollinators, they are relatively immutable within species. By contrast, phenotypic plasticity has high fitness value in vegetative characters because they interface with unpredictable climatic factors. The intrinsic plasticity of vegetative characters makes the recognition of discrete evolutionary units difficult, especially in quantitative characters. As a consequence character selection in this thesis is unavoidably skewed in favour of reproductive characters (46 characters) over vegetative characters (27 characters), and the reproductive characters have clearly dominated in the generation of the trees.

Although the same character states have evolved in widely different areas and in different habitats, distributions do not necessarily provide convincing clues to tracing the evolutionary history of the genus because present distributions may be very different from those of the past.

10.3 CONCLUSIONS

A number of evolutionary pressures have driven divergence of vegetative and floral characters in *Lachenalia*. The convergent adaptation to conditions of aridity appears to be the main reason for homoplasy in whole sets of vegetative characters. Similarly, the convergent modification of flowers to similar pollinators is probably the main reason for homoplasy in whole sets of reproductive characters.

The high degree of convergence in morphological characters in *Lachenalia* was reflected in the overwhelmingly homoplasious results obtained in the cladistic analyses. Most characters were ambiguous as they have evolved more than once, across the genus. The repeated evolution of numerous characters across evolutionary time is probably an indication of their malleable nature, showing rapid genetic drift or having high fitness value in providing expedient solutions to evolutionary problems. Natural selection acting on these characters appears to act quickly, resulting in rapid and continuous modification of characters through the evolutionary history of the genus.

In relation to the large number of taxa analysed, the number of available morphological characters suitable for cladistic analysis is insufficient. With such a high level of homoplasy contained in the consensus trees it is not possible to confidently develop hypotheses on the evolution of most of the characters. However, it is clear that the paraphyletic evolutionary development of *Polyxena* indicates its correct placement within *Lachenalia*.

Speta (1998b) and Pfosser & Speta (1999) have shown that it is difficult to find morphological

characters yielding synapomorphies for groups of taxa within the Hyacinthaceae. In *Lachenalia*, morphological characters alone are insufficient to trace the evolutionary history of the genus, and other approaches such as molecular and cytological methods will be needed in conjunction with morphology in order to generate a robustly supported phylogeny of the genus. However, even these approaches may be insufficient to tease out the rapid radiation that has occurred within the genus. Recent molecular studies on Cape elements of *Oxalis* (Oberlander *et al.* 2004), which have undergone similar rapid massive radiations, have produced molecular results which are similarly plagued with homoplasy.

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Appendix 1. Characters and character states used in the cladistic analyses of <i>Lachenalia</i> and <i>Polyxena</i> , using <i>Massonia</i> as the outgroup	
Characters	States
1. Bulb shape:	globose = 0, subglobose = 1, ovoid = 2
2. Bulb tissue colour:	white = 0, yellow = 1, polymorphic = 2
3. Bulbil production:	non-soboliferous = 0, soboliferous = 1
4. Offset production:	solitary = 0, offset-forming = 1
5. Bulb outer tunic texture:	hard = 0, spongy = 1
6. Bulb apex:	non-extended = 0, extended into distinct neck = 1
7. Bulb apex outer tunics:	fasciculate = 0, non-fasciculate = 1
8. Inner cataphyll apex shape:	obtuse = 0, acute = 1, polymorphic = 2
9. Inner cataphyll adhesion to clasping leaf bases:	non-adhering = 0, adhering = 1, polymorphic = 2
10. Leaf bases:	non-concrescent = 0, concrescent = 1
11. Leaf base markings:	immaculate = 0, banded = 1, spotted = 2
12. Leaf number:	always two = 0, always solitary = 1, one or two = 2, two or more = 3, three or more = 4
13. Leaf orientation:	prostrate = 0, spreading to suberect = 1, erect = 2
14. Pustulate/non-pustulate adaxial leaf surface:	pustules absent = 0, pustules present = 1, polymorphic = 2
15. Adaxial leaf trichomes:	trichomes absent = 0, trichomes simple = 1, trichomes stellate = 2
16. Adaxial leaf maculation:	always immaculate = 0, always maculate = 1, polymorphic = 2
17. Leaf shape:	ovate = 0, lanceolate = 1, linear = 2
18. Distal lamina profile:	flat = 0, canaliculate = 1, convex = 2
19. Basal lamina profile:	flat = 0, canaliculate = 1
20. Adaxial leaf tertiary sculpturing:	finely striate = 0, laevigate = 1, median longitudinally ridged = 2, median longitudinally ridged and sides transversely ridged = 3, median finely striate and sides transversely ridged = 4, transversely ridged = 5
21. Abaxial leaf tertiary sculpturing:	finely striate = 0, laevigate = 1, median longitudinally ridged = 2, transversely ridged = 3
22. Leaf margin anatomy:	simple margin = 0, flabellate margin = 1, 'polyxena' margin = 2, multiple epidermis margin = 3, sclerotic margin = 4
23. Leaf margin shape:	flat = 0, crisped = 1
24. Leaf margin vestiture:	glabrous = 0, ciliolate = 1, ciliate = 2, stellate = 3
25. Leaf apex shape:	naviculate = 0, acute = 1

Appendix 1. Characters and character states used in the cladistic analyses of <i>Lachenalia</i> and <i>Polyxena</i> , using <i>Massonia</i> as the outgroup	
Characters	States
26. Primary seedling leaf orientation:	prostrate = 0, suberect = 1, erect = 2
27. Primary seedling leaf shape:	flat = 0, terete = 1
28. Peduncle elevation at anthesis:	subterranean = 0, aerial = 1
29. Peduncle inflation:	non-swollen in upper half = 0, distinctly swollen in upper half = 1, polymorphic = 2
30. Rachis apical anthocyanins:	absent = 0, present = 1
31. Rachis apical carotenoids:	absent = 0, present = 1
32. Rachis apical chlorophylls:	absent = 0, present = 1
33. Rachis apex structural white:	present = 0, absent = 1
34. Lower bract shape:	ovate = 0, cup-shaped = 1
35. Upper bract shape:	lanceolate = 0, ovate = 1, cup-shaped = 2
36. Inflorescence type:	racemose = 0, spicate = 1, polymorphic = 2
37. Pedicel orientation at anthesis:	erect = 0, suberect = 1, patent = 2, curved downwards = 3, absent = 4
38. Perianth shape (tepal orientation):	tubular = 0, oblong-campanulate = 1, narrowly campanulate = 2, widely campanulate = 3, urceolate = 4
39. Perianth tube length:	long = 0, short = 1
40. Perianth tube shape:	tubular = 0, cup-shaped = 1, disc-shaped = 2
41. Flower arrangement:	spiral = 0, three-flowered whorls = 1
42. Outer tepal shape:	oblong = 0, ovate = 1
43. Outer tepal length:	short = 0, long = 1
44. Outer tepal apex:	recurved = 0, flat = 1
45. Inner tepal shape:	linear-oblong = 0, obovate = 1, oblong-obovate = 2
46. Inner tepal length:	short = 0, long = 1
47. Inner and outer tepal arrangement:	inner and outer tepals subequal = 0, inner tepals longer than outer tepals = 1
48. Floral symmetry:	actinomorphic = 0, zygomorphic = 1
49. Ventral inner tepal extension:	protrudes equally with upper inner tepals = 0, shorter than upper inner tepals = 1, protrudes beyond upper inner tepals = 2
50. Filament orientation at anthesis:	straight = 0, narrowly spreading = 1, recurved = 2, declinate = 3
51. Filament colour:	white = 0, white in lower half, purple or magenta in upper half = 1, polymorphic = 2

Appendix 1. Characters and character states used in the cladistic analyses of <i>Lachenalia</i> and <i>Polyxena</i> , using <i>Massonia</i> as the outgroup	
Characters	States
52. Filament length:	short = 0, long = 1
53. Filament relative lengths:	equal = 0, subequal = 1
54. Outer filament insertion:	upper = 0, medial = 1, basal = 2
55. Inner filament insertion:	upper = 0, medial = 1
56. Pollen exine sculpturing:	rugose = 0, reticulate = 1
57. Style orientation at anthesis:	straight = 0, declinate = 1
58. Ovary shape:	obovoid = 0, ellipsoid = 1
59. Capsule shape:	obovoid = 0, ellipsoid = 1, ovoid = 2, obcordate = 3
60. Capsule orientation:	retains same orientation as flower orientation = 0, bends upwards to suberect or erect position = 1, bends downwards to hanging position = 2
61. Capsule length:	short = 0, long = 1
62. Inflorescence elongation:	elongated = 0, non-elongated = 1
63. Testa lustre:	glossy black = 0, matte black = 1
64. Seed length:	medium = 0, short = 1, long = 2
65. Seed width:	medium = 0, narrow = 1, wide = 2
66. Seed shape:	globose = 0, ovoid = 1, oblong = 2
67. Testa primary sculpturing:	smooth = 0, rugose = 1
68. Testa secondary sculpturing:	absent = 0, reticulate = 1, colliculate = 2
69. Strophiole length:	rudimentary = 0, medium = 1, long = 2
70. Strophiole texture:	ridged = 0, smooth = 1
71. Strophiole inflation:	non-inflated = 0, inflated = 1
72. Raphe inflation:	non-inflated = 0, inflated = 1
73. Chalazal collar length:	absent = 0, short = 1, long = 2

Appendix 2. Data matrix used for the cladistic analyses of *Lachenalia* and *Polyxena*, using *Massonia* as the outgroup

Massonia00000 00000 00000 00000 00000 00000 00000 00000 00000 00000 00000 00000 00000 00000 000
L. alba00011 00010 00100 01010 01000 21101 00101 01111 01011 01122 00110 10110 01100 10010 000
L. algoensis00011 01000 00100 21112 21000 00101 00100 01000 00112 11100 00110 10110 01000 00021 100
L. aloides var. *aloides*20011 01000 00100 21012 11000 21101 10100 01000 00112 11100 01121 10111 11000 00021 100
L. aloides var. *aurea*00011 01010 00100 11012 11000 00100 10100 01000 00112 11100 01121 10111 11000 00021 100
L. aloides var. *bonaspei*00011 01000 00100 11012 11000 00101 10100 01000 00112 11100 01121 10111 11000 00021 100
L. aloides var. *luteola*00011 01000 00100 21012 11000 00101 10100 01000 00112 11100 00121 10111 01000 00021 100
L. aloides var. *piketbergensis*20011 01000 00100 01012 11000 00100 10100 01000 00112 11100 01121 10111 11000 00021 100

Appendix 2. Data matrix used for the cladistic analyses of *Lachenalia* and *Polyxena*, using *Massonia* as the outgroup

L. aloides var. *quadricolor*.....20011 01000 00100 21012 11000 21101 10100 01000 00112 11100 01121 10111 11000 00021 100
L. aloides var. *thunbergii*00011 01010 00100 01012 11000 21101 10100 01000 00112 11100 00121 10111 01000 00021 100
L. aloides var. *vanzyliae*.....00011 01010 20100 11012 11000 00101 00100 01000 00112 11100 00121 10111 01000 00021 100
L. ameliae.....00001 11010 22101 01000 10020 21101 00101 14411 01001 01123 00110 11110 01100 10010 001
L. angelica.....00001 01100 01002 01001 30030 00100 00012 02311 01001 00103 00110 01000 01111 00100 000
L. anguinea10011 01000 11100 01110 00001 21111 00100 01211 01011 00103 00110 11000 01002 00000 000
L. arbuthnotiae.....10011 01000 22100 11112 21000 00100 10100 14111 01011 01100 00110 10110 01000 00011 100
L. arida.....00000 10010 00100 02115 12000 21101 00112 02311 01010 00101 00010 10000 01002 00000 000

Appendix 2. Data matrix used for the cladistic analyses of *Lachenalia* and *Polyxena*, using *Massonia* as the outgroup

L. attenuata10001 01000 11100 02110 02000 21101 00101 01111 01011 00120 00110 10000 01100 10020 000
L. aurioliae.....20011 00010 22100 11011 11000 21101 00101 01411 11011 01103 00110 11110 01100 10020 000
L. bachmannii10011 01000 00100 02110 12001 21101 00112 01211 01011 01100 00010 10110 01000 00000 000
L. barkeriana.....00001 01001 04100 02112 20000 00010 00001 00011 00010 01100 00110 10110 00000 00011 101
L. bolusii00011 01000 11100 01111 30100 21101 00101 01411 01011 01120 00110 10000 01100 01011 101
L. bowkeri10010 00010 02100 01110 31000 11100 01100 01111 01011 01100 00110 10110 01100 00110 000
L. buchbergensis20001 01010 11100 01110 00100 21101 00100 01011 01011 00100 00110 10130 01120 21000 002
L. bulbifera.....10111 01020 02100 20013 12000 21101 10101 01000 00112 10110 01121 10110 11000 00021 110

Appendix 2. Data matrix used for the cladistic analyses of *Lachenalia* and *Polyxena*, using *Massonia* as the outgroup

L. campanulata20011 01100 20100 22111 02001 21101 00112 01311 01000 00102 00010 10000 01000 00000 000
L. canaliculata00010 00100 22100 01112 01000 21101 00101 14111 11011 01123 00110 11110 01000 10010 000
L. capensis.....10011 01000 02100 21015 11000 00101 00100 24011 01011 01110 00110 10110 01000 00011 100
L. carnososa12001 01010 00120 20013 01000 00101 00100 14411 01011 01123 00110 11110 01000 10000 001
L. cernua00011 01??0 22100 11013 21000 00101 00100 01111 01011 01100 00110 10110 01000 00021 100
L. comptonii00001 01100 02101 01011 00020 21101 00112 01311 01000 00102 10010 10110 01000 00000 000
L. concordiana00000 10100 11100 01115 20000 21101 00100 14111 11011 01123 00110 11110 01100 10010 001
L. congesta00001 11010 00000 00004 02000 00001 00100 14411 01001 01100 00110 10110 01022 00000 000

Appendix 2. Data matrix used for the cladistic analyses of *Lachenalia* and *Polyxena*, using *Massonia* as the outgroup

L. contaminata var. *contaminata*10011 01000 04200 12202 00001 21101 00112 01211 01010 00100 00110 10111 01000 00000 000
L. contaminata var. *exserta*.....10011 01000 04200 02202 00001 21101 00112 01211 01010 00100 00110 10111 01000 00000 000
L. convallarioides10011 01100 01100 01111 10001 21101 00112 01211 01011 00100 00010 10000 01000 00000 000
L. dasybotrya.....00000 00010 00100 00003 02000 21101 00100 01111 01011 01123 00110 11110 01100 10010 000
L. dehoopensis.....00010 10010 12100 02115 11000 00101 00100 01111 01011 01100 00110 10110 01100 00110 000
L. doleritica.....20000 10010 00100 20011 01000 ??101 00100 01111 01011 01120 00110 10010 01022 10020 000
L. duncanii20000 10000 00100 21111 14100 21101 00100 01111 01011 01103 10110 11000 01000 10010 001
L. elegans var. *elegans*00011 01100 02100 01013 21000 00101 00100 14411 01011 00100 00110 10000 01000 00011 100

Appendix 2. Data matrix used for the cladistic analyses of *Lachenalia* and *Polyxena*, using *Massonia* as the outgroup

L. elegans var. *flava*00011 01100 22100 11013 21000 00101 00100 14411 11011 00100 00110 10110 01000 00011 100
L. elegans var. *membranacea*.....00011 01100 22100 11013 21000 00101 00100 14411 11011 00100 00110 10110 01000 00011 100
L. elegans var. *suaveolens*.....00011 01100 22100 01013 21000 00101 00100 14411 11011 00100 00110 10110 01000 00011 100
L. esterhuysenae.....00011 011?0 02100 0221? ??001 ??10? ???01 02111 01011 00100 00110 ?0000 01000 00000 000
L. fasciculata.....20000 10010 11100 10000 01000 21101 00101 14111 11011 01120 00110 10110 01100 10010 001
L. fistulosa.....10011 01000 02100 21013 11000 00101 00100 14411 01011 01100 00110 10110 01000 00011 100
L. framesii10011 01010 02100 01111 20100 21101 00100 14411 01011 01123 00110 11110 01000 10100 001
L. giessii00000 10010 00100 01015 12010 21101 00112 02311 01010 00101 00010 10000 01002 00000 000

Appendix 2. Data matrix used for the cladistic analyses of *Lachenalia* and *Polyxena*, using *Massonia* as the outgroup

L. gillettii.....11011 01010 02100 01013 21000 00101 00100 01111 01011 01123 00110 11110 01000 00000 000
L. glauca00011 01000 02100 01112 21000 21111 00101 01111 01011 00100 00110 10110 01000 00111 100
L. glaucophylla00001 01110 01100 01113 30000 21101 00112 01311 01000 00102 00010 10000 01000 10010 001
L. haarlemensis10011 01000 11200 01112 21000 21101 00101 01111 01011 01100 10110 10000 01000 00010 000
L. hirta var. *hirta*.....10011 01000 11100 02110 00020 11101 00100 01111 01011 00120 00110 10001 01100 00100 000
L. hirta var. *exserta*10011 01000 11100 0211? ?0020 11101 00100 01111 01011 00120 00110 10001 01100 00100 000
L. inconspicua00001 10010 11100 11111 21000 21101 00100 14111 11011 01120 00110 10110 01100 10120 000
L. isopetala.....00000 10010 00100 01111 12100 21101 00101 01011 00110 00100 00110 00110 01022 00000 000

Appendix 2. Data matrix used for the cladistic analyses of *Lachenalia* and *Polyxena*, using *Massonia* as the outgroup

L. juncifolia var. *juncifolia*.....10011 01010 10100 02210 00001 21101 00101 01111 01011 00100 00110 00000 01000 00000 000
L. juncifolia var. *campanulata*10011 01010 10100 02210 00001 21101 00101 02211 01011 00100 00110 00000 01000 00000 000
L. karooica20001 00110 12100 11111 11000 21101 00100 21111 01011 01102 00110 10110 01000 10120 000
L. klinghardtiana.....00011 01000 21100 01112 11100 21111 00100 01111 01011 01123 00110 11110 01000 00010 001
L. kliprandensis.....21001 01010 00000 10003 01000 00001 00100 14211 01011 01123 00110 11110 01000 10010 000
L. komsbergensis.....10001 01010 11100 01112 22100 21101 00100 01111 01011 01100 00110 00000 01100 01010 000
L. lactosa.....00011 01000 02100 01011 31000 00101 00100 01111 01011 01100 00110 10111 01000 00011 100
L. latimerae.....10011 01010 22100 01110 01000 21101 00101 01111 01011 01100 00110 10000 01000 00010 000

Appendix 2. Data matrix used for the cladistic analyses of *Lachenalia* and *Polyxena*, using *Massonia* as the outgroup

L. leipoldtii.....00001 01110 21100 01113 21000 11101 00100 01111 01011 01103 00110 11110 01000 00011 100
L. leomontana00011 01010 01100 11011 11000 00101 00100 01111 01011 01100 00110 10001 01000 00011 100
L. liliiflora11011 01000 00110 01010 21000 00101 00112 01211 01011 01101 00110 10110 01000 10000 000
L. longibracteata.....00011 01010 22100 11011 21000 00101 00100 24111 01011 01100 00110 10110 01000 00011 100
L. lutea00011 01010 02100 01013 21000 00101 00100 14111 01011 01100 00110 10110 01000 00011 100
L. macgregoriorum00011 01010 20100 01112 22000 21101 00112 01311 01010 00102 10010 00000 01100 00000 000
L. margaretae.....01011 01100 02100 21012 20000 00101 00100 01111 01011 00100 00110 10000 01000 00011 100
L. marginata subsp. *marginata*10011 01000 11100 10012 21100 00101 00100 14000 01011 01120 00110 10110 01000 00011 100

Appendix 2. Data matrix used for the cladistic analyses of *Lachenalia* and *Polyxena*, using *Massonia* as the outgroup

L. marginata subsp. *neglecta*10011 01000 11100 11013 21100 00101 00100 14111 01011 01120 00110 10110 01000 00011 100
L. marlothii00001 01000 11100 01013 21100 00101 00100 24111 11011 01120 00110 10110 01002 10020 101
L. martinae00000 00000 11100 01011 11100 21101 00100 01111 01011 01110 00110 10110 01000 00011 100
L. mathewsii00011 01010 00100 02211 10001 21101 00101 01111 01011 00123 00110 11111 01000 10000 000
L. maximiliani20010 01010 01100 01110 00000 21101 00100 01111 01011 00120 00110 10110 01000 10010 000
L. mediana var. *mediana*00011 01010 02100 01112 11000 00101 00100 01111 01011 01123 00110 11111 01000 00021 100
L. mediana var. *rogersii*20011 01010 12100 01110 11100 00101 00100 01111 01011 01123 00110 11111 01000 00021 100
L. minima00010 10100 00110 01012 11000 21101 00100 14111 01001 01100 00110 10110 01000 10010 001

Appendix 2. Data matrix used for the cladistic analyses of *Lachenalia* and *Polyxena*, using *Massonia* as the outgroup

L. moniliformis 10111 01000 14200 02200 00001 21101 00101 01111 01011 00103 00110 11000 01000 00000 000
L. montana 00011 01010 00100 02110 00001 21101 00100 03111 01011 01100 00110 10001 01100 00200 000
L. muirii 00011 01000 00100 11112 11000 00101 00101 14411 01010 01102 00110 10000 01011 00011 100
L. multifolia 00011 01110 04200 02200 10001 21101 00112 02311 01000 00101 00010 00002 01000 00000 000
L. mutabilis 10011 01000 01100 01112 21000 21121 00100 14411 01011 01123 00110 11110 01000 00011 101
L. namaquensis 00111 01010 02100 02210 22001 21101 00101 14411 01011 01123 00110 11110 01000 10110 000
L. namibiensis 20010 00010 02100 01114 20010 21101 00112 02311 01010 00101 00010 00000 01000 00000 000
L. nardouwensis 11011 01010 00100 11013 01000 00101 00100 01111 01011 00103 00110 11110 01000 00011 000

Appendix 2. Data matrix used for the cladistic analyses of *Lachenalia* and *Polyxena*, using *Massonia* as the outgroup

L. neilii00011 00010 00100 21010 02000 21101 00101 01111 01011 01122 00110 10110 01102 10010 000
L. nervosa.....10001 01210 00020 00001 14000 00101 00100 01311 01000 00102 00010 10001 01000 00011 100
L. nordenstamii20001 110?0 11100 01110 10000 ??101 00100 03311 01000 00101 10010 ?0130 01120 20000 002
L. nutans.....00001 01?10 01100 0111? ??000 ??11? ???00 01111 01011 00103 00110 ?1000 01000 00000 000
L. obscura00010 00000 12100 11112 01000 21101 00101 24111 11011 01100 00110 10110 01000 10010 000
L. orchioides var. *orchioides*00011 01010 02100 11012 21000 00101 00100 14000 01012 11100 00110 10110 01000 00011 100
L. orchioides var. *glaucina*00011 01010 02100 11012 21000 00101 00100 14000 01012 11100 00110 10110 01000 00011 100
L. orthopetala.....11011 01010 04100 22112 02001 21101 00112 01211 01011 01101 00110 10110 01000 10000 000

Appendix 2. Data matrix used for the cladistic analyses of *Lachenalia* and *Polyxena*, using *Massonia* as the outgroup

L. patula00010 00010 00200 02211 10001 00100 00012 01311 01011 01103 00110 01110 01111 01000 001
L. pearsonii00000 00010 00100 02115 20010 21101 00112 02311 01010 00001 00010 10000 01022 00000 000
L. peersii10011 01000 02100 01012 21000 00101 00100 01411 01011 01100 00110 00001 01000 00011 100
L. perryae00011 01000 11100 01112 11000 21101 00101 01111 01011 01120 00110 10000 01100 10110 001
L. physocaulos00001 01110 01100 01112 21000 11111 00100 01111 01011 01103 10110 11110 01000 00011 100
L. polyphylla00011 01010 04200 02201 10011 21101 00112 01111 01011 00102 00110 00001 01101 01000 000
L. polypodantha00001 01100 01102 01005 10030 00101 00112 02311 01011 01103 10110 11001 01100 00100 000
L. purpureocaerulea11011 01010 00110 01000 01000 00101 00101 01111 01011 00103 10110 11111 01000 00000 000

Appendix 2. Data matrix used for the cladistic analyses of *Lachenalia* and *Polyxena*, using *Massonia* as the outgroup

L. pusilla00001 01011 04000 11003 21000 00000 00001 00011 00010 01100 00110 10110 00000 00011 101
L. pustulata11011 01010 02120 01013 01000 00101 00100 01111 01011 01123 00110 11111 01000 00000 000
L. reflexa.....10011 01210 02100 21111 21100 21101 00100 00000 00011 01110 00100 10110 10000 00011 100
L. rosea.....10011 01010 02100 21112 21000 00101 00100 01111 01011 01100 00110 00001 01000 00011 100
L. rubida.....00011 01000 22100 11112 22000 00101 00101 01000 00112 11110 01121 10110 11000 00011 111
L. salteri10001 01010 02100 21112 11000 00101 00100 01111 01011 01120 00110 00111 01000 00011 100
L. sargeantii00011 01010 00100 02110 00001 ??10? ???00 03011 00112 11100 00110 ?0001 01100 00200 000
L. schelpei20011 00010 10100 11010 01000 00101 00100 01011 01011 00100 00110 10110 01120 10020 000

Appendix 2. Data matrix used for the cladistic analyses of *Lachenalia* and *Polyxena*, using *Massonia* as the outgroup

L. splendida.....01011 01000 02100 01014 01000 21101 00100 14111 01011 01123 10110 11110 01000 10000 000
L. stayneri00001 01000 00010 01001 03000 00101 00100 01111 01011 00100 00110 10000 01000 00011 100
L. thomasiae.....11011 01000 02100 01010 20000 00101 00100 01111 01011 01123 00110 11110 01000 00011 100
L. trichophylla subsp. *trichophylla*10001 01010 01002 00001 10030 00101 00101 14000 10011 01120 00110 00110 01111 00100 001
L. trichophylla subsp. *massonii*10001 01010 01002 00001 10030 00101 00101 01000 00011 01120 00110 00110 01111 00100 001
L. undulata subsp. *undulata*.....20000 10000 00100 11113 12100 21100 01100 14111 01011 01100 00110 10110 01100 10010 001
L. undulata subsp. *grandifolia*20000 10000 00100 01110 02000 21100 01100 14111 01011 01100 00110 10110 01100 10010 001
L. unicolor.....11011 01100 00110 01013 01000 00101 00100 01111 01011 00103 00110 11110 01000 00000 000

Appendix 2. Data matrix used for the cladistic analyses of *Lachenalia* and *Polyxena*, using *Massonia* as the outgroup

L. unifolia var. *unifolia*10011 01010 11100 02110 10001 21101 00100 01111 00011 01120 00110 00111 01000 00000 000
L. unifolia var. *schlechteri*10011 01010 11100 02110 10001 21101 00100 01111 00011 01120 00110 00110 01000 00000 000
L. urceolata00010 10100 10100 01012 20000 21101 00100 14411 11011 01100 00110 10110 01000 00010 000
L. valeriae10001 01010 02110 01015 20000 11101 00100 14411 01011 01123 00110 11110 01000 10000 001
L. variegata10011 01000 22100 21012 21100 00101 00100 01111 01011 00103 00110 11110 01000 00021 100
L. ventricosa11001 01000 01100 01112 21100 11111 00100 14011 01011 01100 00110 10110 01000 10011 101
L. verticillata20001 01100 11100 21112 23100 21101 00100 14411 11011 01123 00110 11110 01100 10010 001
L. violacea20011 01100 22100 21112 21100 21111 00101 01111 01011 00100 10110 10110 01000 00011 100

Appendix 2. Data matrix used for the cladistic analyses of *Lachenalia* and *Polyxena*, using *Massonia* as the outgroup

L. viridiflora10011 01210 02100 21111 21000 21101 00100 01000 00011 01110 00100 10110 11100 00011 100
L. whitehillensis10001 01010 11100 01110 21000 21101 00101 01111 01011 00103 00110 11000 01100 10010 000
L. wiesei00011 01000 11100 01012 21100 21101 00101 02111 11011 01100 00110 10110 01100 11010 000
L. xerophila00001 01??0 02100 0111? ??100 2111? ???00 01111 01011 01103 00110 ?1000 01020 20000 011
L. youngii00011 01110 00100 02112 11001 21101 00100 01111 01011 00100 00110 10001 01000 00011 100
L. zebrina20001 11010 11100 01111 20100 21101 00101 01112 01011 00100 00110 10130 01122 10010 001
L. zeyheri10011 01010 02100 02211 02001 21101 00112 01211 01011 00100 00010 10000 01000 00000 000
Polyxena corymbosa10011 01010 03100 02113 10001 00101 00100 00000 00000 00000 00110 00000 00100 11000 000

Appendix 2. Data matrix used for the cladistic analyses of *Lachenalia* and *Polyxena*, using *Massonia* as the outgroup

Polyxena ensifolia.....10011 01010 00100 01003 12010 21000 00000 00000 00000 00002 20100 00120 00000 10000 000
Polyxena longituba00011 01010 00100 01113 20011 21000 00000 00000 00000 00000 00100 00120 00000 10000 000
Polyxena maughanii.....10011 01010 00100 01002 02010 21000 00000 00000 00000 00000 00100 00120 00000 10000 000
Polyxena paucifolia.....00011 01010 02100 02112 00001 00101 00100 00000 00000 00000 00100 00000 00100 00000 000

Appendix 3. Occurrence and distribution of pigments in the tepals of <i>Lachenalia</i> and <i>Polyxena</i>					
Taxa	Chlorophylls	Xanthophylls	Carotenoids	Anthocyanins	Structural white
<i>L. alba</i>	inner and outer mesophyll, pale green in outer tepal gibbositities	absent	absent	absent, or magenta in outer mesophyll, outer tepal tips and inner tepal keels; blue in outer tepal bases	aerenchymatous tissue in inner and outer mesophyll, inner and outer tepals
<i>L. algoensis</i>	inner and outer mesophyll, pale green in outer tepal gibbositities	inner and outer mesophyll, pale yellow in inner and outer tepals	absent	absent	absent
<i>L. aloides</i> var. <i>aloides</i>	inner and outer mesophyll, bright green in outer tepal gibbositities	absent	inner and outer mesophyll, bright yellow in inner and outer tepals	outer mesophyll, red in inner tepal bases and tips	absent
<i>L. aloides</i> var. <i>aurea</i>	inner and outer mesophyll, pale green in outer tepal gibbositities	absent	inner and outer mesophyll, bright orange in inner and outer tepals	absent	absent
<i>L. aloides</i> var. <i>bonaspei</i>	inner and outer mesophyll, bright green in outer tepal gibbositities	absent	inner and outer mesophyll, bright yellow in inner and outer tepals	epidermal, magenta in inner tepal tips; outer mesophyll, red in outer tepal bases	absent
<i>L. aloides</i> var. <i>luteola</i>	inner and outer mesophyll, pale green in outer tepal gibbositities and inner and outer tepals	inner mesophyll, pale yellow in inner and outer tepals	absent	absent	absent
<i>L. aloides</i> var. <i>piketbergensis</i>	inner and outer mesophyll, bright green in inner tepal keels and outer tepal gibbositities	absent	inner and outer mesophyll, bright yellow in inner and outer tepals	absent	absent
<i>L. aloides</i> var. <i>quadricolor</i>	inner and outer mesophyll, bright green in outer tepal gibbositities	absent	inner and outer mesophyll, bright yellow in inner and outer tepals	epidermal, magenta in inner tepal tips; outer mesophyll, red in outer tepal bases	absent
<i>L. aloides</i> var. <i>thunbergii</i>	inner and outer mesophyll, pale green in inner tepal keels and outer tepal gibbositities	absent	inner and outer mesophyll, bright yellow in inner and outer tepals	absent	absent
<i>L. aloides</i> var. <i>vonzyliae</i>	inner and outer mesophyll, bright green in inner tepal tips and outer tepal gibbositities	absent	absent	outer mesophyll, blue in outer tepal bases	absent
<i>L. ameliae</i>	inner and outer mesophyll, pale green in outer tepal gibbositities and inner tepal keels	inner and outer mesophyll, pale yellow in inner and outer tepals	absent	absent, or magenta in mesophyll, inner tepal keels and outer tepal tips	absent

Appendix 3. Occurrence and distribution of pigments in the tepals of *Lachenalia* and *Polyxena*

Taxa	Chlorophylls	Xanthophylls	Carotenoids	Anthocyanins	Structural white
<i>L. angelica</i>	inner and outer mesophyll, pale green in outer tepal gibbosities	absent	absent	absent	aerenchymatous tissue in inner and outer mesophyll, inner and outer tepals
<i>L. anguinea</i>	inner and outer mesophyll, pale to bright green in outer tepal gibbosities	absent or in inner and outer mesophyll, pale yellow in inner and outer tepals	absent	absent	aerenchymatous tissue in inner and outer mesophyll, inner and outer tepals
<i>L. arbuthnotiae</i>	inner and outer mesophyll, pale green in outer tepal gibbosities	absent	inner and outer mesophyll, bright yellow in inner and outer tepals	absent	absent
<i>L. arida</i>	inner and outer mesophyll, pale green in outer tepal gibbosities	absent	absent	absent	aerenchymatous tissue in inner and outer mesophyll, inner and outer tepals
<i>L. attenuata</i>	inner and outer mesophyll, pale green in outer tepal gibbosities	absent	absent	outer mesophyll, blue in inner and outer tepals	absent
<i>L. auriolae</i>	inner and outer mesophyll, pale green in outer tepal gibbosities	absent	absent	outer mesophyll, blue in inner and outer tepals	absent
<i>L. bachmannii</i>	inner and outer mesophyll, pale green in inner tepal keels and outer tepal gibbosities	absent	absent	outer mesophyll, magenta in outer tepal gibbosities and inner tepal keels	aerenchymatous tissue in inner and outer mesophyll, inner and outer tepals
<i>L. barkeriana</i>	inner and outer mesophyll, pale green in inner tepal keels and outer tepal gibbosities	absent	absent	absent	aerenchymatous tissue in inner and outer mesophyll, inner and outer tepals
<i>L. bolusii</i>	inner and outer mesophyll, pale green in outer tepal gibbosities	absent	absent	outer mesophyll, blue in inner and outer tepals; magenta in inner tepal keels and outer tepal gibbosities	absent
<i>L. bowkeri</i>	inner and outer mesophyll, pale green in inner and outer tepals	absent	absent	outer mesophyll, magenta in inner tepal keels and outer tepal gibbosities	absent
<i>L. buchubergensis</i>	inner and outer mesophyll, pale green in outer tepal gibbosities	absent	absent	outer mesophyll, magenta in inner tepal tips; blue in inner and outer tepals	absent
<i>L. bulbifera</i>	inner and outer mesophyll, bright green in inner tepal tips and outer tepal gibbosities	absent	inner mesophyll, bright yellow in inner and outer tepals	outer mesophyll, red in inner and outer tepals	absent

Appendix 3. Occurrence and distribution of pigments in the tepals of <i>Lachenalia</i> and <i>Polyxena</i>					
Taxa	Chlorophylls	Xanthophylls	Carotenoids	Anthocyanins	Structural white
<i>L. campanulata</i>	inner and outer mesophyll, pale green in outer tepal gibbosities	absent	absent	outer mesophyll, bluish-pink in inner and outer tepals	absent
<i>L. canaliculata</i>	inner and outer mesophyll, pale green in outer tepal gibbosities	absent	absent	outer mesophyll, pale blue in inner and outer tepals	absent
<i>L. capensis</i>	inner and outer mesophyll, pale green in outer tepal gibbosities	absent, or in inner and outer mesophyll, pale yellow in inner and outer tepals	absent	absent, or blue in outer mesophyll and outer tepal bases	aerenchymatous tissue in inner and outer mesophyll, inner and outer tepals
<i>L. carnosa</i>	inner and outer mesophyll, dark green in outer tepal gibbosities	absent	absent	outer mesophyll, bright magenta in inner and outer tepal tips; pale blue in outer tepal bases	aerenchymatous tissue in inner and outer mesophyll, inner and outer tepals
<i>L. cernua</i>	inner and outer mesophyll, bright green in outer tepal gibbosities	inner and outer mesophyll, pale yellow in inner and outer tepals	absent	absent	absent
<i>L. comptonii</i>	inner and outer mesophyll, bright green in inner tepal keels and outer tepal gibbosities	absent	absent	outer mesophyll, dull pink in inner tepal keels and outer tepal gibbosities	aerenchymatous tissue in inner and outer mesophyll, inner and outer tepals
<i>L. concordiana</i>	inner and outer mesophyll, pale green in inner tepal keels and outer tepal gibbosities	inner and outer mesophyll, pale yellow in inner and outer tepals	absent	outer mesophyll, pale blue in outer tepal bases	absent
<i>L. congesta</i>	inner and outer mesophyll, bright green in inner tepal keels and outer tepal gibbosities	inner and outer mesophyll, pale yellow in inner and outer tepals	absent	outer mesophyll, pale blue in outer tepal bases	absent
<i>L. contaminata</i> var. <i>contaminata</i>	inner and outer mesophyll, pale green in outer tepal gibbosities	absent	absent	outer mesophyll, magenta in inner tepal keels and outer tepal gibbosities	aerenchymatous tissue in inner and outer mesophyll, inner and outer tepals
<i>L. contaminata</i> var. <i>exserta</i>	inner and outer mesophyll, pale green in outer tepal gibbosities	absent	absent	outer mesophyll, magenta in inner tepal keels and outer tepal gibbosities	aerenchymatous tissue in inner and outer mesophyll, inner and outer tepals
<i>L. convallarioides</i>	inner and outer mesophyll, pale green in outer tepal gibbosities	absent	absent	outer mesophyll, pale magenta in inner and outer tepals	aerenchymatous tissue in inner and outer mesophyll, inner and outer tepals
<i>L. dasybotrya</i>	inner and outer mesophyll, pale green in outer tepal gibbosities	absent	absent	outer mesophyll, pale blue in outer tepal bases	aerenchymatous tissue in inner and outer mesophyll, inner and outer tepals

Appendix 3. Occurrence and distribution of pigments in the tepals of <i>Lachenalia</i> and <i>Polyxena</i>					
Taxa	Chlorophylls	Xanthophylls	Carotenoids	Anthocyanins	Structural white
<i>L. dehoopensis</i>	inner and outer mesophyll, pale green in outer tepal gibbositics	absent	absent	outer mesophyll, magenta in inner tepal keels and outer tepal gibbositics	aerenchymatous tissue in inner and outer mesophyll, inner and outer tepals
<i>L. doleritica</i>	inner and outer mesophyll, pale green in outer tepal gibbositics	inner and outer mesophyll, pale yellow in inner and outer tepals	absent	outer mesophyll, pale blue in outer tepal bases	absent
<i>L. duncanii</i>	inner and outer mesophyll, dark green in inner tepal keels and outer tepal gibbositics	absent	absent	outer mesophyll, magenta in inner tepal keels	absent
<i>L. elegans</i> var. <i>elegans</i>	inner and outer mesophyll, dark green in outer tepal gibbositics	absent	absent	outer mesophyll, bright blue in inner and outer tepals	aerenchymatous tissue in inner and outer mesophyll, inner tepal tips
<i>L. elegans</i> var. <i>flava</i>	absent	absent	inner and outer mesophyll, bright yellow in inner and outer tepals	outer mesophyll, dark magenta in inner tepal tips and outer tepal gibbositics	aerenchymatous tissue in inner and outer mesophyll, inner tepal tips
<i>L. elegans</i> var. <i>membranacea</i>	inner and outer mesophyll, pale green in outer tepal gibbositics	absent	inner and outer mesophyll, bright yellow in inner and outer tepals	outer mesophyll, pale magenta in inner tepal keels and outer tepal gibbositics	aerenchymatous tissue in inner and outer mesophyll, inner tepal tips
<i>L. elegans</i> var. <i>suaveolens</i>	absent	absent	absent	outer mesophyll, deep magenta in inner tepal keels and outer tepal gibbositics	aerenchymatous tissue in inner and outer mesophyll, inner tepal tips
<i>L. fasciculata</i>	inner and outer mesophyll, pale green in inner tepal keels	absent	absent	outer mesophyll, blue in outer tepal bases and keels	absent
<i>L. fistulosa</i>	inner and outer mesophyll, pale green in outer tepal gibbositics	absent	absent	outer mesophyll, pale pink or blue in inner and outer tepals	aerenchymatous tissue in inner and outer mesophyll, inner and outer tepals
<i>L. framesii</i>	inner and outer mesophyll, bright green in outer tepal gibbositics	absent	inner and outer mesophyll, bright yellow in inner and outer tepals	outer mesophyll, bright magenta in inner tepal tips	absent
<i>L. giessii</i>	inner and outer mesophyll, pale green in inner tepal keels and outer tepal gibbositics	absent	absent	outer mesophyll, pale magenta in inner tepal keels	aerenchymatous tissue in inner and outer mesophyll, inner and outer tepals
<i>L. gillettii</i>	inner and outer mesophyll, dark green in outer tepal gibbositics	absent	absent	outer mesophyll, bright magenta in inner tepal keels and outer tepal gibbositics	absent

Appendix 3. Occurrence and distribution of pigments in the tepals of <i>Lachenalia</i> and <i>Polyxena</i>					
Taxa	Chlorophylls	Xanthophylls	Carotenoids	Anthocyanins	Structural white
<i>L. glauca</i>	absent	absent	absent	outer mesophyll, pale to deep magenta in inner and outer tepals	absent
<i>L. glaucophylla</i>	inner and outer mesophyll, pale green in outer tepal gibbosities	absent	absent	outer mesophyll, pale blue in outer tepal bases	aerenchymatous tissue in inner and outer mesophyll, inner and outer tepals
<i>L. haarlemensis</i>	inner and outer mesophyll, pale green in outer tepal tips	absent	absent	outer mesophyll, pale blue in inner and outer tepals	absent
<i>L. hirta</i> var. <i>hirta</i>	inner and outer mesophyll, pale green in inner and outer tepal tips	absent	absent	outer mesophyll, dark magenta in outer tepal gibbosities and inner tepal keels; blue in inner and outer tepals	absent
<i>L. inconspicua</i>	inner and outer mesophyll, dark green in outer tepal gibbosities	absent	absent	outer mesophyll, pale blue in inner and outer tepals	aerenchymatous tissue in inner and outer mesophyll, inner tepal tips
<i>L. isopetala</i>	inner mesophyll, pale green in inner tepal keels, outer tepal gibbosities and keels	inner and outer mesophyll, pale yellow in inner and outer tepals	absent	outer mesophyll, magenta in inner tepal keels, outer tepal gibbosities and keels	absent
<i>L. juncifolia</i> var. <i>juncifolia</i>	inner and outer mesophyll, pale green in outer tepal gibbosities	absent	absent	outer mesophyll, magenta in inner and outer tepals	absent
<i>L. karooica</i>	inner and outer mesophyll, pale green in outer tepal gibbosities	absent	absent	outer mesophyll, pale blue in inner and outer tepals	aerenchymatous tissue in inner and outer mesophyll, inner tepals
<i>L. klinghardtiana</i>	inner and outer mesophyll, pale green in inner tepal keels and outer tepal gibbosities	absent	absent	outer mesophyll, pale blue in outer tepal bases	aerenchymatous tissue in inner and outer mesophyll, inner and outer tepals
<i>L. kliprandensis</i>	inner and outer mesophyll, pale green in outer tepal gibbosities	absent	absent	outer mesophyll, bright magenta in inner and outer tepal tips and keels	absent
<i>L. komsbergensis</i>	inner and outer mesophyll, pale green in outer tepal gibbosities	absent	absent	outer mesophyll, pale blue in inner and outer tepals	aerenchymatous tissue in inner and outer mesophyll, inner tepal tips
<i>L. lactosa</i>	inner and outer mesophyll, pale green in outer tepal gibbosities	absent	absent	absent, or in outer mesophyll, magenta in inner and outer tepals	aerenchymatous tissue in inner and outer mesophyll, inner and outer tepals

Appendix 3. Occurrence and distribution of pigments in the tepals of <i>Lachenalia</i> and <i>Polyxena</i>					
Taxa	Chlorophylls	Xanthophylls	Carotenoids	Anthocyanins	Structural white
<i>L. latimerae</i>	inner and outer mesophyll, pale green in outer tepal gibbosities	absent	absent	outer mesophyll, pale pink in inner and outer tepals	absent
<i>L. leipoldtii</i>	inner and outer mesophyll, pale green in outer tepal gibbosities	absent	absent	outer mesophyll, pale blue in inner and outer tepals	absent
<i>L. leomontana</i>	inner and outer mesophyll, pale green in outer tepal gibbosities	absent	absent	outer mesophyll, pale blue in outer tepal bases	aerenchymatous tissue in inner and outer mesophyll, inner and outer tepals
<i>L. liliiflora</i>	inner and outer mesophyll, dark green in outer tepal gibbosities	absent	absent	outer mesophyll, dark magenta in outer tepal gibbosities and inner tepal tips	aerenchymatous tissue in inner and outer mesophyll, inner and outer tepals
<i>L. longibracteata</i>	inner and outer mesophyll, pale green in inner tepal keels and outer tepal gibbosities	absent	absent	outer mesophyll, pale blue in inner and outer tepals	absent
<i>L. lutea</i>	inner and outer mesophyll, pale green in inner tepal keels and outer tepal gibbosities	absent	inner and outer mesophyll, bright yellow in inner and outer tepals	absent	absent
<i>L. macgregoriorum</i>	absent	absent	absent	outer mesophyll, dark magenta in inner and outer tepal keels and gibbosities	absent
<i>L. margaretae</i>	inner and outer mesophyll, pale green in inner tepal keels and outer tepal gibbosities	absent	absent	outer mesophyll, dark magenta in outer tepal gibbosities and inner tepal keels	aerenchymatous tissue in inner and outer mesophyll, inner and outer tepals
<i>L. marginata</i> subsp. <i>marginata</i>	inner and outer mesophyll, bright green in inner tepal keels	inner and outer mesophyll, pale yellow in inner tepal tips	absent	outer mesophyll, dark magenta in outer tepal gibbosities	absent
<i>L. marginata</i> subsp. <i>neglecta</i>	inner and outer mesophyll, pale green in inner tepal keels	inner and outer mesophyll, pale yellow in inner tepal tips	absent	outer mesophyll, dark magenta in outer tepal gibbosities	absent
<i>L. marlothii</i>	inner and outer mesophyll, pale green in inner tepal keels and outer tepal gibbosities	inner and outer mesophyll, pale yellow in inner tepals	absent	outer mesophyll, dark magenta in outer tepal gibbosities; pale blue in outer tepal bases	absent
<i>L. martinae</i>	inner and outer mesophyll, pale green in outer tepal gibbosities	absent	absent	outer mesophyll, blue in inner and outer tepals; magenta in outer tepal keels	aerenchymatous tissue in inner and outer mesophyll, outer tepals

Appendix 3. Occurrence and distribution of pigments in the tepals of <i>Lachenalia</i> and <i>Polyxena</i>					
Taxa	Chlorophylls	Xanthophylls	Carotenoids	Anthocyanins	Structural white
<i>L. mathewsii</i>	inner and outer mesophyll, bright green in inner tepal keels and outer tepal gibbosities	absent	inner and outer mesophyll, bright yellow in inner and outer tepals	absent	absent
<i>L. maximiliani</i>	inner and outer mesophyll, pale green in outer tepal gibbosities	absent	absent	outer mesophyll, pale blue in outer tepal bases; magenta in outer tepal gibbosities	aerenchymatous tissue in inner and outer mesophyll, inner tepals
<i>L. mediana</i> var. <i>mediana</i>	inner and outer mesophyll, pale green in inner tepal keels and outer tepal gibbosities	absent	absent	outer mesophyll, pale blue in outer tepal bases	absent
<i>L. mediana</i> var. <i>rogersii</i>	inner and outer mesophyll, pale green in outer tepal gibbosities	absent	absent	outer mesophyll, pale blue in inner and outer tepals; dark magenta in outer tepal gibbosities and inner tepal keels	aerenchymatous tissue in inner and outer mesophyll, inner tepal tips
<i>L. minima</i>	inner and outer mesophyll, dark green in inner tepal keels and outer tepal gibbosities	inner mesophyll, pale yellow in inner and outer tepals	absent	absent	absent
<i>L. moniliformis</i>	absent	absent	absent	outer mesophyll, pale blue in outer tepal bases; magenta in outer tepal gibbosities and inner tepal keels	absent
<i>L. montana</i>	inner and outer mesophyll, bright green in inner tepal keels and outer tepal gibbosities	absent	absent	outer mesophyll, pale magenta in outer tepal bases; dark magenta in outer tepal tips	absent
<i>L. mairii</i>	inner and outer mesophyll, dark green in outer tepal gibbosities	absent	absent	outer mesophyll, pale blue in outer tepal bases; magenta and pink in outer tepal gibbosities and inner tepal keels	aerenchymatous tissue in inner and outer mesophyll, inner and outer tepals
<i>L. multifolia</i>	inner and outer mesophyll, pale green in inner tepal keels and outer tepal gibbosities	absent	absent	absent	aerenchymatous tissue in inner and outer mesophyll, inner and outer tepals

Appendix 3. Occurrence and distribution of pigments in the tepals of <i>Lachenalia</i> and <i>Polyxena</i>					
Taxa	Chlorophylls	Xanthophylls	Carotenoids	Anthocyanins	Structural white
<i>L. mutabilis</i>	absent	inner and outer mesophyll, pale yellow in inner and outer tepals	absent	outer mesophyll, deep magenta in outer tepal gibbositities and inner tepal keels; pale blue in outer tepal bases	absent
<i>L. namaquensis</i>	inner and outer mesophyll, dark green in outer tepal gibbositities	absent	absent	outer mesophyll, dark pink in inner and outer tepals; deep magenta in outer tepal gibbositities and keels	absent
<i>L. namibiensis</i>	inner and outer mesophyll, pale green in outer tepal gibbositities	absent	absent	outer mesophyll, pale magenta in inner tepal keels	aerenchymatous tissue in inner and outer mesophyll, inner and outer tepals
<i>L. nardouwensis</i>	inner and outer mesophyll, dark green in outer tepal gibbositities	absent	absent	outer mesophyll, bright pink in inner and outer tepals; dark magenta in outer tepal gibbositities and inner tepal keels	absent
<i>L. neilii</i>	inner and outer mesophyll, bright green in inner tepal keels and outer tepal gibbositities	absent	absent	outer mesophyll, pale blue in outer tepal bases	aerenchymatous tissue in inner and outer mesophyll, inner tepals
<i>L. nervosa</i>	inner and outer mesophyll, pale green in outer tepal gibbositities	absent	absent	outer mesophyll, magenta in outer tepal gibbositities and inner tepal keels	absent
<i>L. obscura</i>	inner and outer mesophyll, dark green in inner tepal keels and outer tepal gibbositities	absent	absent	outer mesophyll, bright magenta in inner tepal tips; pale blue in outer tepal bases	absent
<i>L. orchioides</i> var. <i>orchioides</i>	inner and outer mesophyll, pale green in inner tepal keels and outer tepal gibbositities	inner and outer mesophyll, pale yellow in inner and outer tepals	absent	outer mesophyll, pale blue in outer tepal bases	absent
<i>L. orchioides</i> var. <i>glaucina</i>	absent	absent	absent	outer mesophyll, pale to dark blue in outer tepal bases, outer tepal gibbositities and inner tepal tips	absent

Appendix 3. Occurrence and distribution of pigments in the tepals of <i>Lachenalia</i> and <i>Polyxena</i>					
Taxa	Chlorophylls	Xanthophylls	Carotenoids	Anthocyanins	Structural white
<i>L. orthopetala</i>	absent	absent	absent	outer mesophyll, dark magenta in outer tepal gibbosities and inner tepal keels	aerenchymatous tissue in inner and outer mesophyll, inner and outer tepals
<i>L. patula</i>	absent	absent	absent	inner and outer mesophyll, pink or dark magenta in outer tepal gibbosities and inner tepal keels	aerenchymatous tissue in inner and outer mesophyll, inner and outer tepals
<i>L. pearsonii</i>	inner and outer mesophyll, pale green in inner tepal keels and outer tepal gibbosities	absent	absent	outer mesophyll, magenta in outer tepal gibbosities and inner tepal keels	aerenchymatous tissue in inner and outer mesophyll, inner and outer tepals
<i>L. peersii</i>	inner and outer mesophyll, dark green in outer tepal gibbosities	absent	absent	outer mesophyll, magenta in outer tepal gibbosities	aerenchymatous tissue in inner and outer mesophyll, inner and outer tepals
<i>L. perryae</i>	inner and outer mesophyll, pale green in inner tepal keels and outer tepal gibbosities	absent	absent	outer mesophyll, magenta in outer tepal gibbosities; pale blue in outer tepal bases and tips	aerenchymatous tissue in inner and outer mesophyll, inner tepals
<i>L. physocaulos</i>	absent	absent	absent	outer mesophyll, dark magenta in outer tepal gibbosities and inner tepal keels; pale pink in inner tepal tips	absent
<i>L. polyphylla</i>	inner and outer mesophyll, pale green in inner tepal keels and outer tepal gibbosities	absent	absent	outer mesophyll, dark magenta in outer tepal gibbosities and inner tepal keels; blue in outer tepal bases	aerenchymatous tissue in inner and outer mesophyll, inner and outer tepals
<i>L. polypodantha</i>	inner and outer mesophyll, dark green in inner tepal tips and outer tepal gibbosities	absent	absent	outer mesophyll, dark purple, outer and inner tepals	absent
<i>L. purpureocaerulea</i>	inner and outer mesophyll, dark green in outer tepal gibbosities	absent	absent	outer mesophyll, dark magenta, outer tepal gibbosities and inner and outer tepal tips	aerenchymatous tissue in inner and outer mesophyll, inner and outer tepals
<i>L. pusilla</i>	inner and outer mesophyll, pale green in inner and outer tepal keels	absent	absent	absent	aerenchymatous tissue in inner and outer mesophyll, inner and outer tepals

Appendix 3. Occurrence and distribution of pigments in the tepals of <i>Lachenalia</i> and <i>Polyxena</i>					
Taxa	Chlorophylls	Xanthophylls	Carotenoids	Anthocyanins	Structural white
<i>L. pustulata</i>	inner and outer mesophyll, absent or dark green in inner tepal keels and outer tepal gibbositities	absent	absent	outer mesophyll, pale to deep pink, magenta or purple in outer tepal gibbositities and inner tepal keels; blue in outer tepal bases	absent, or aerenchymatous tissue in inner and outer mesophyll, inner and outer tepals
<i>L. reflexa</i>	inner and outer mesophyll, pale green in inner tepal keels and outer tepal gibbositities	absent	inner and outer mesophyll, bright yellow in inner and outer tepals	absent	absent
<i>L. rosea</i>	absent	absent	absent	inner and outer mesophyll, pale to deep pink in outer tepal gibbositities and inner tepal keels; pale blue in outer tepal bases	absent
<i>L. rubida</i>	absent	absent	absent	outer mesophyll, bright pink in inner and outer tepals	absent
<i>L. salteri</i>	absent	absent	absent	inner and outer mesophyll, deep magenta in outer tepal gibbositities and inner tepal keels; pale pink in inner and outer tepal tips, bright blue in outer tepal bases	absent
<i>L. schelpei</i>	inner mesophyll, pale green in outer tepal gibbositities and inner tepal keels	absent	absent	outer mesophyll, pale blue in outer tepal bases and keels	absent
<i>L. splendida</i>	inner mesophyll, dark green in outer tepal gibbositities	absent	absent	outer mesophyll, deep magenta in outer tepal gibbositities and inner tepal tips and keels; pale blue in outer tepal bases	absent
<i>L. stayneri</i>	absent	absent	absent	outer mesophyll, dark magenta in outer tepal gibbositities and inner tepal keels; pale blue in outer tepal bases	aerenchymatous tissue in inner and outer mesophyll, inner tepals

Appendix 3. Occurrence and distribution of pigments in the tepals of <i>Lachenalia</i> and <i>Polyxena</i>					
Taxa	Chlorophylls	Xanthophylls	Carotenoids	Anthocyanins	Structural white
<i>L. thomasiae</i>	inner mesophyll, bright green in outer tepal gibbositics and inner tepal keels	absent	absent	outer mesophyll, dark magenta in outer tepal gibbositics and inner tepal keels	aerenchymatous tissue in inner and outer mesophyll, inner and outer tepals
<i>L. trichophylla</i> subsp. <i>trichophylla</i>	inner mesophyll, pale green in outer tepal gibbositics	inner and outer mesophyll, pale yellow in inner and outer tepals	absent	absent	absent
<i>L. trichophylla</i> subsp. <i>massonii</i>	inner mesophyll, pale green in outer tepal gibbositics and inner tepal tips	absent	absent	outer mesophyll, pale magenta in outer tepal bases	absent
<i>L. undulata</i> subsp. <i>undulata</i>	inner mesophyll, dark green in outer tepals and outer tepal gibbositics	absent	absent	outer mesophyll, dark magenta in outer tepal gibbositics and inner tepal keels; pale blue in outer tepal bases	aerenchymatous tissue in inner and outer mesophyll, inner tepals
<i>L. undulata</i> subsp. <i>grandifolia</i>	inner mesophyll, dark green in outer tepals and outer tepal gibbositics	absent	absent	outer mesophyll, dark magenta in outer tepal gibbositics and inner tepal keels; pale blue in outer tepal bases	aerenchymatous tissue in inner and outer mesophyll, inner tepals
<i>L. unicolor</i>	inner mesophyll, dark green in outer tepal gibbositics	absent	absent	outer mesophyll, pale to dark magenta or purple in outer tepal gibbositics, inner tepal keels and tips	absent
<i>L. unifolia</i> var. <i>unifolia</i>	inner mesophyll, pale green in outer tepal gibbositics	absent	absent	outer mesophyll, pale blue or pale pink in outer tepal bases and gibbositics	aerenchymatous tissue in inner and outer mesophyll, inner tepals and outer tepal tips
<i>L. urceolata</i>	inner mesophyll, pale green in outer tepal bases and inner tepal keels	absent	absent	outer mesophyll, dark magenta in outer tepal gibbositics and inner tepal keels	aerenchymatous tissue in inner and outer mesophyll, inner tepals
<i>L. valeriae</i>	inner mesophyll, bright green in outer tepals and gibbositics, and inner tepal keels	absent	absent	outer mesophyll, bright magenta in upper half of ventral inner tepal; pale blue in outer tepal bases	absent
<i>L. variegata</i>	inner mesophyll, pale green in outer tepal gibbositics	absent	absent	outer mesophyll, pale blue in outer tepal bases	absent

Appendix 3. Occurrence and distribution of pigments in the tepals of <i>Lachenalia</i> and <i>Polyxena</i>					
Taxa	Chlorophylls	Xanthophylls	Carotenoids	Anthocyanins	Structural white
<i>L. ventricosa</i>	absent	inner mesophyll, pale yellow in inner tepal tips	absent	outer mesophyll, dark magenta in outer tepal gibbositities and inner tepal keels	absent
<i>L. verticillata</i>	inner mesophyll, pale green in outer tepal gibbositities	absent	absent	outer mesophyll, pale blue in outer tepal bases and keels; purple in inner tepal tips	absent
<i>L. violacea</i>	inner mesophyll, pale green in inner and outer tepals	absent	absent	outer mesophyll, pale blue in outer tepal bases and keels; purple in inner tepal tips	absent
<i>L. viridiflora</i>	absent	absent	absent	epidermal, dark blue in outer tepal gibbositities and keels; pale blue in inner and outer tepals	absent
<i>L. whitehillensis</i>	absent	absent	absent	outer mesophyll, dark magenta in outer tepal gibbositities and inner tepal keels; pale blue in outer tepals	aerenchymatous tissue in inner and outer mesophyll, inner tepal tips
<i>L. wiesei</i>	absent	absent	absent	outer mesophyll, magenta in outer tepal gibbositities and inner tepal keels; pale blue in outer tepal bases	absent
<i>L. youngii</i>	inner mesophyll, pale green in outer tepal gibbositities, inner tepal keels	absent	absent	inner and outer mesophyll, pink in outer tepals, magenta in outer tepal gibbositities and inner tepal keels; pale blue in outer tepal bases	absent
<i>L. zebrina</i>	inner mesophyll, pale green in outer tepal gibbositities and inner tepal keels	absent	absent	outer mesophyll, magenta in outer tepal gibbositities, inner tepal keels and in inner and outer tepals	absent
<i>L. zeyheri</i>	inner mesophyll, pale green in outer tepal gibbositities and inner tepal keels	absent	absent	outer mesophyll, magenta in outer tepal gibbositities and inner tepal keels	aerenchymatous tissue in inner and outer mesophyll, inner and outer tepals

Appendix 3. Occurrence and distribution of pigments in the tepals of <i>Lachenalia</i> and <i>Polyxena</i>					
Taxa	Chlorophylls	Xanthophylls	Carotenoids	Anthocyanins	Structural white
<i>P. corymbosa</i>	absent	absent	absent	outer mesophyll, dark magenta in inner and outer tepal keels; pink in inner and outer tepals	aerenchymatous tissue in inner and outer mesophyll, inner and outer tepals
<i>P. ensifolia</i>	inner mesophyll, pale green in inner and outer tepal keels	absent	absent	absent or in outer mesophyll, deep magenta in inner and outer tepal keels; pale magenta in inner and outer tepals	absent, or aerenchymatous tissue in inner and outer mesophyll, inner and outer tepals
<i>P. longituba</i>	absent	absent	absent	outer mesophyll, deep magenta in inner and outer tepal keels, bright magenta in inner and outer tepals	aerenchymatous tissue in inner and outer mesophyll, inner and outer tepals
<i>P. maughanii</i>	absent	absent	absent	outer mesophyll, pale magenta in outer tepal tips	aerenchymatous tissue in inner and outer mesophyll, inner and outer tepals
<i>P. paucifolia</i>	absent	absent	absent	outer mesophyll, bright magenta in inner and outer tepals	absent