Phytogeography of the subtribe Leipoldtiinae (Mesembryanthemaceae)

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ABSTRACT

An investigation of distribution and species frequency of the nine genera of the subtribe Leipoldtiinae shows that two centres of diversity can be distinguished. These coincide more or less with the 'Gariep centre' in the north and the 'Vanrhynsdorp centre' in the south (both sensu Nordenstam 1969). Speciation seems to have occurred in both centres. The subtribe may have evolved in an arid winter rainfall area which could have been situated outside its present distribution area. The centres of distribution coincide with those observed in both subfamilies of the Mesembryanthemaceae.

UITTREKSEL

'n Ondersoek na verspreiding en spesie-frekwensie van die nege genusse van die subtribus Leipoldtiinae toon dat twee sentrums van diversiteit onderskei kan word. Hierdie twee kom min of meer ooreen met die 'Gariepsentrum' in die noorde en die 'Vanrhynsdorpsentrum' in die suide (albei sensu Nordenstam 1969). Dit wil voorkom asof spesiasie in albei sentrums plaasgevind het. Die subtribus kon moontlik in 'n dorre winterreëngebied wat buite die huidige verspreidingsgebied geleë kon gewees het, ontwikkel het. Die verspreidingsentrums kom ooreen met dié wat in albei subfamilies van die Mesembryanthemaceae waargeneem is.

INTRODUCTION

The subtribe Leipoldtiinae of the Mesembryanthemaceae comprises nine genera with a total of 81 species. Members of the subtribe can be recognized by their rather hard xeromorphic leaves (the outer epidermal wall always contains calcium oxalate crystals) and their multilocular capsules (Figure 1) with valve wings, closing bodies and complete covering membranes. These membranes are distally recurved and radially traversed by a trace of spongy tissue which distally forms an additional closing device (closing bulge, ledge or rod, Hartmann 1983c). Dissemination depends directly on the described internal structure (Funktionstyp 1 after Hartmann 1983c) and is effected in most taxa only by rain drops.

This is the first analysis of its kind within the Mesembryanthemaceae because this is the first group of genera for which adequate data are available. The phytogeography of the subtribe is of particular interest for two reasons: the distribution area of the Leipoldtiinae coincides with the centre of distribution of the entire family; and within this area, members of the subtribe form a major part of the vegetation.

METHODS AND MATERIAL

The investigation is based on numerous field studies carried out between 1977 and 1986, about 6 000 relevant collections and about 800 additional herbarium sheets. Ecological data are derived partly from literature and partly from own observations; rainfall data were provided by the Weather Bureau, Pretoria. Information concerning morphology, anatomy, evolution and detailed distribution are taken from the relevant genus monographs (see References).

RESULTS

Distribution of the subtribe

The subtribe is confined to the south-western Cape. Only one genus *(Cephalophyllum)* occurs in the entire range of the subtribe (see Figure 2), the other genera are restricted to smaller areas. The frequency distribution of genera is consequently uneven (Figure 3). Two main centres can be distinguished, a southern one, which will be referred to as 'Vanrhynsdorp centre' (sensu Nordenstam 1969), and a northern one, which agrees largely with the 'Gariep centre' (sensu Nordenstam 1969). These centres stand out even more prominently when species distribution (Figure 4) is considered, and their significance will be discussed below.
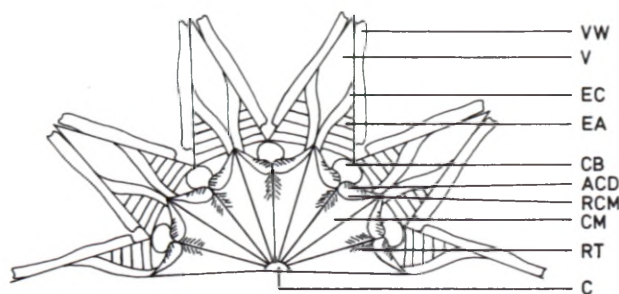

FIGURE 1. — Open fruit of Leipoldtiinae, schematic. ACD = additional closing device; C = columella; CB = closing body; CM = covering membrane; EA = expanding area; EC = expanding keel; RCM = recurved distal portion of covering membrane; RT = radial trace of spongy tissue; V = valve; VW = valve wing.

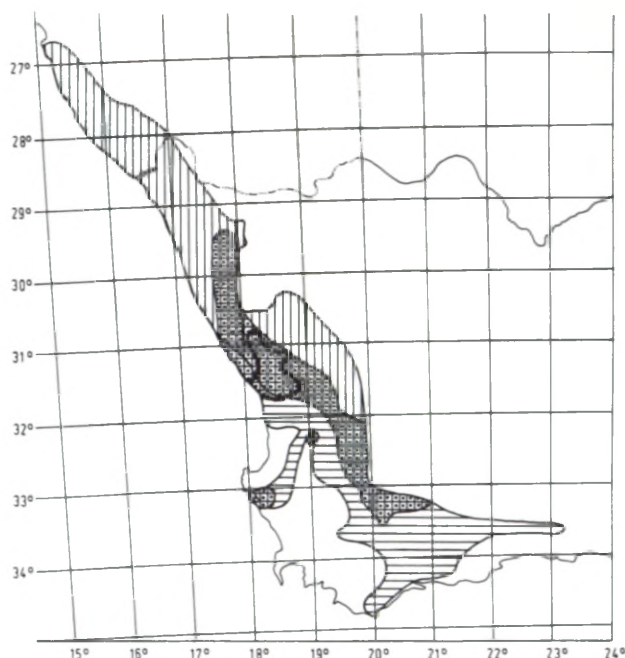* Institut für Allgemeine Botanik, Universität Hamburg, Ohnhorststrasse 18, D-2000 Hamburg 52, West Germany.

FIGURE 2. — Distribution areas of *Cephalophyllum* (thin lines) and *Argyroderma* (bold line). Horizontal lines = *Cephalophyllum* subgenus *Cephalophyllum*; vertical lines = *Cephalophyllum* subgenus *Homophyllum*; overlapping areas dotted.
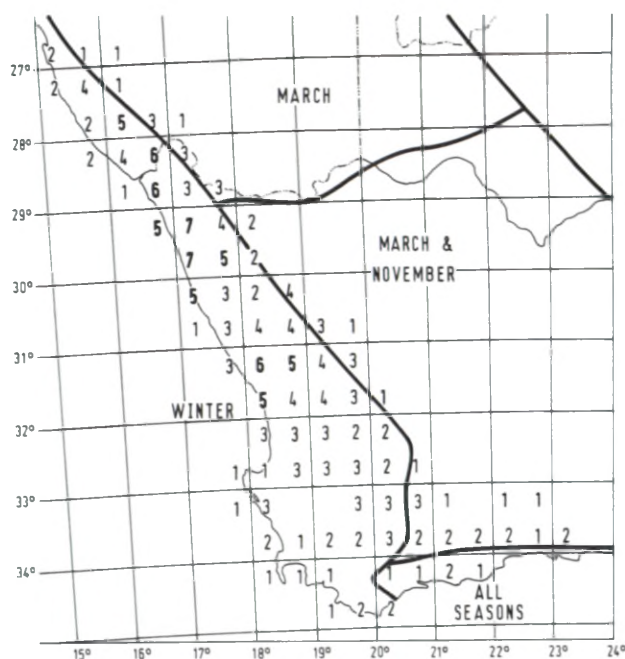

FIGURE 4. — Frequency of species of Leipoldtiinae (N = 81) per 30′ × 30′ square. The same two centres as in Figure 3 stand out (bold figures).

fall areas. Only two species out of the 81 have their centre of distribution outside the winter rainfall region: *Cephalophyllum subulatoides* (Haw.) N.E. Br. (southern Little Karoo, 33°30′S, 21°–23°E) and *Cheiridopsis caroli-schmidtii* (Dinter & Berger) N.E. Br. (near Aus, 27°S, 16°E). The amount of annual precipitation decreases in the distribution area from south to north, and less markedly from west to east (Figure 5).

Phytochorologically, the main concentration of taxa falls into the Western Cape Domain of the Karoo-Namib Region as defined by Werger (1978), with extensions into the Namib Domain in the north, into the Karoo Domain in the north-east and even into Capensis in the south (Figure 4). Only a few species have their centre of distribution in Capensis sensu Werger (1978), namely *Cephalophyllum diversiphyllum* (Haw.) H. E. K. Hartm., *C. loreum* (L.) Schwantes, and *C. subulatoides* (Haw.) N.E. Br.

Distribution of genera

Cephalophyllum

The largest genus of the subtribe, *Cephalophyllum* N.E. Br., with 30 species, has the largest distribution area (Figure 2) and grows in a wide range of ecological situations, from coastal to high mountain habitats, from monotypic open succulent associations to undergrowth in fynbos, and from the highest to the lowest rainfall regimes in different seasons. The two subgenera have different centres of distribution (Figure 2): subgenus *Cephalophyllum* dominates in the south and subgenus *Homophyllum* in the north, with a wide corridor in which they overlap.

A species frequency analysis (based on numbers of species per 30′ × 30′ square) reveals that the highest number of species occurs in the Vanrhynsdorp centre (Figure 6), which lies in the zone of overlap of the subgenera (Figure 2). A second centre of species

FIGURE 3. — Frequency of genera of Leipoldtiinae (N = 9) per 30′ × 30′ square. Two centres can be distinguished: 'Gariep centre' (bold figures between latitudes 27° and 31°); 'Vanrhynsdorp centre' (bold figures between latitudes 31° and 32°). Bold lines delineate the four main rainfall areas of the region.

The eastern limit of the distribution area of the Leipoldtiinae coincides for most of its extension with the eastern boundary of the winter rainfall area (defined here as the region receiving at least 60% of its annual precipitation between April and September, Figure 3). Only in the south, three genera *(Cephalophyllum, Jordaaniella* and *Leipoldtia)* extend considerably into the March/November or all season rain-
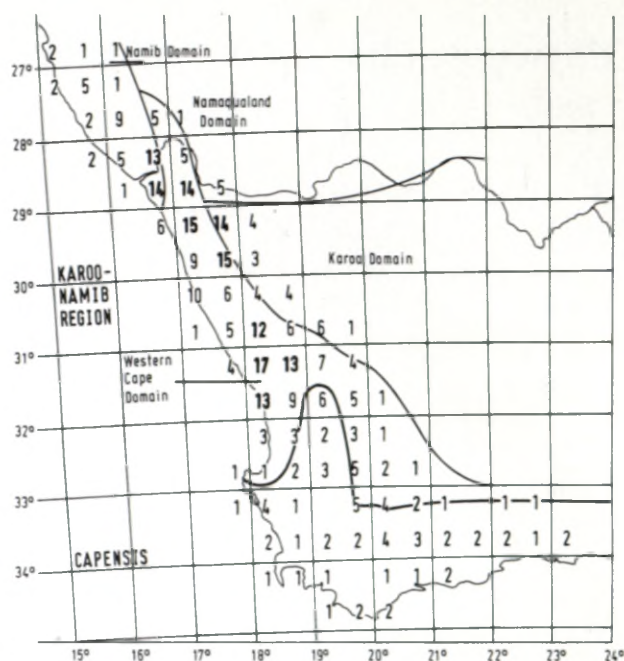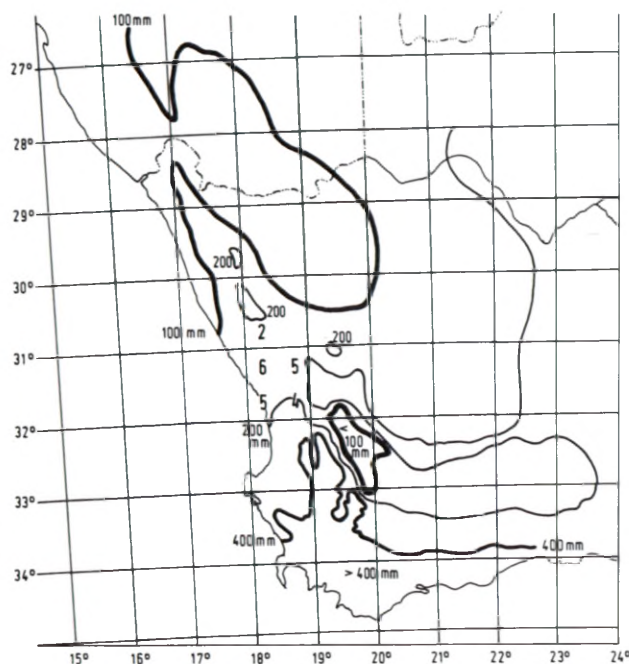
FIGURE 5. — Frequency of species of *Argyroderma* (N = 10) per 30′ × 30′ square and selected isohyets (bold line = 100 mm; medium line = 400 mm; thin line = 200 mm).

frequency lies in the north and coincides with the Gariep centre of the subtribe (Figure 3). These centres cannot be correlated directly with the subgenera, as the centre of subgenus *Cephalophyllum* is situated near 33°S, 20°E (Figure 6 and Hartmann in press). In spite of the high species numbers per square, sympatry in *Cephalophyllum* is rare and speciation has been predominantly allopatric (Hartmann in press). Twelve species (40%) can be considered endemic: they occur in one to three 30′ squares only (Figure 6). They are found near the two species centres but their frequency is low (1–3 per 30′ square).
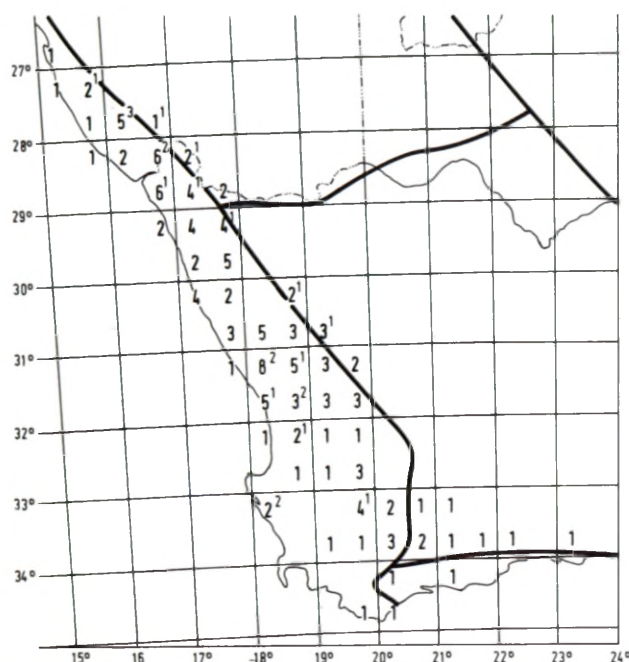
Consequently, *Cephalophyllum* can be described as a genus with mostly widespread yet vicariant species, which have become adapted to a wide range of edaphic and climatic conditions: the genus occurs in 13 different vegetation types as defined by Acocks (1975) (Hartmann in press). The extended distribution area reflects the high degree of adaptability of the genus even today, supporting the hypothesis that the genus is at present in an active evolutionary phase (Hartmann in press).

Argyroderma

Closely related to *Cephalophyllum* is the genus *Argyroderma* N.E. Br. (Hartmann 1983c, in press) with ten species (Hartmann 1978a), restricted in distribution to the Knersvlakte in the Vanrhynsdorp centre (Figure 2), with a maximum of six species per 30′ square (Figure 5). In contrast to *Cephalophyllum*, *Argyroderma* therefore presents a genus of narrow distribution which is due to the strict adaptation to the unique edaphic mosaic of the Knersvlakte.

Leipoldtia

With only eight species, *Leipoldtia* L. Bol. is one of the smaller genera of the subtribe, yet it is one of wide distribution (Figure 7). The predominantly shrubby plants often grow in conspicuous patches, mostly on gravelly and flat sedimentary soils. In contrast to the wide occurrence of subgenus *Leipoldtia*, the subgenera *Aureae* and *Cephalophylloides* inhabit only restricted areas overlapping with that of subgenus *Leipoldtia* (Figure 7). Only one species (*L. frutescens*, of the subgenus *Aureae*) grows in coastal plains (Strandveld sensu Acocks 1975). All other taxa inhabit higher altitudes, mainly in Namaqualand Broken Veld, Western Mountain Karoo and Karroid Broken Veld of the Little Karoo.

FIGURE 6. — Frequency of species of *Cephalophyllum* (N = 30) per 30′ × 30′ square. Small figures indicate frequency of endemic species.
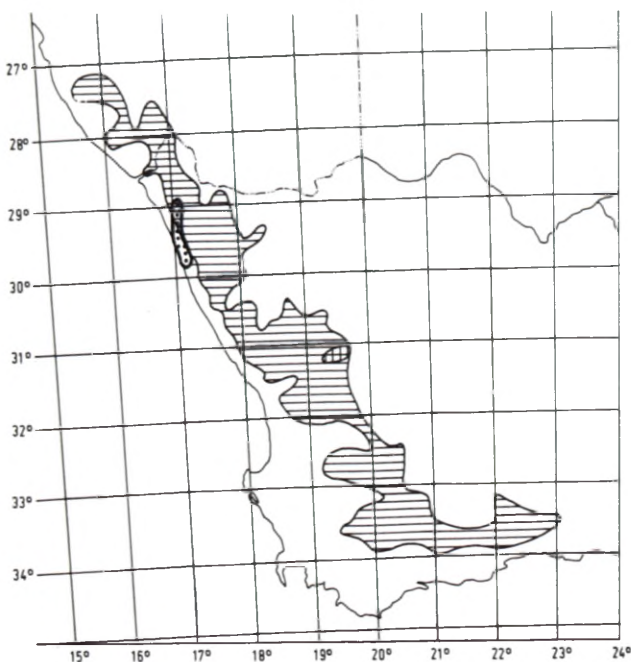

FIGURE 7. — Distribution area of *Leipoldtia*. Horizontal lines = subgenus *Leipoldtia;* vertical lines = subgenus *Cephalophylloides;* dots = subgenus *Aureae.*
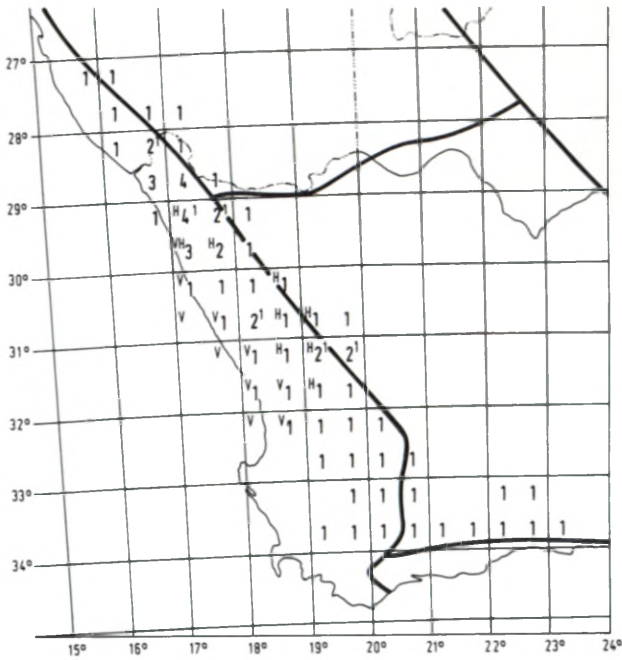
FIGURE 8. — Frequency of species of *Leipoldtia* (N = 8) per 30′ × 30′ square. H = occurrence of *Hallianthus;* V = occurrence of *Vanzijlia* in the square.

The highest species frequencies are found within the southern Gariep centre (Figure 8), where in certain localities up to three species occur sympatrically, each fitting into an ecological niche slightly different from those of the others (Hartmann & Rust in prep.). Since the same species can inhabit obviously different habitats in distant areas, a fine regulation of adaptation in regard to competition and isolation can be expected, but this is not yet understood (Rust unpublished).

Although 50% of all species of *Leipoldtia* occur in one 30′ square, it cannot be simply assumed that this area presents a centre of origin. The scattered distribution of endemic species (Figure 8), and the varied character expressions in geographically separated areas of one species, point more towards an active phase of speciation by means of differentiation of semi-isolated, more or less marginal populations. The high species frequency in the Gariep centre could be the result of secondary invasions combined with the stabilization of hybrid derivatives as ecologically well adapted forms which have become isolated (Rust unpublished).

Hallianthus and *Vanzijlia*

Two monotypic genera with allopatric distribution are related to the genus *Leipoldtia* (Hartmann 1983c): *Hallianthus* H. E. K. Hartm. and *Vanzijlia* L. Bol. *Hallianthus* grows predominantly at altitudes above 300 m (Hartmann 1983b) in Namaqualand Broken Veld (sensu Acocks 1975) in associations of succulent shrubs. It extends northwards into the Gariep centre (Figure 8). *Vanzijlia*, as a mainly coastal genus, occurs around and in the Vanrhynsdorp centre (Figure 8). Most populations have been found in shrubby succulent associations of the Strandveld (sensu Acocks 1975), few inland in Succulent Karoo (Hartmann 1983a).

Cheiridopsis and *Odontophorus*

The genus *Cheiridopsis* N.E. Br. with 23 species, represents the third of the widespread genera of the subtribe. Like the genus *Odontophorus* N.E. Br., it can be recognized by its papillose leaf surface (Hartmann 1983c). As in *Cephalophyllum*, the two larger subgenera (subgenus *Cheiridopsis* and *Aequifoliae)* inhabit largely different geographical areas (Figure
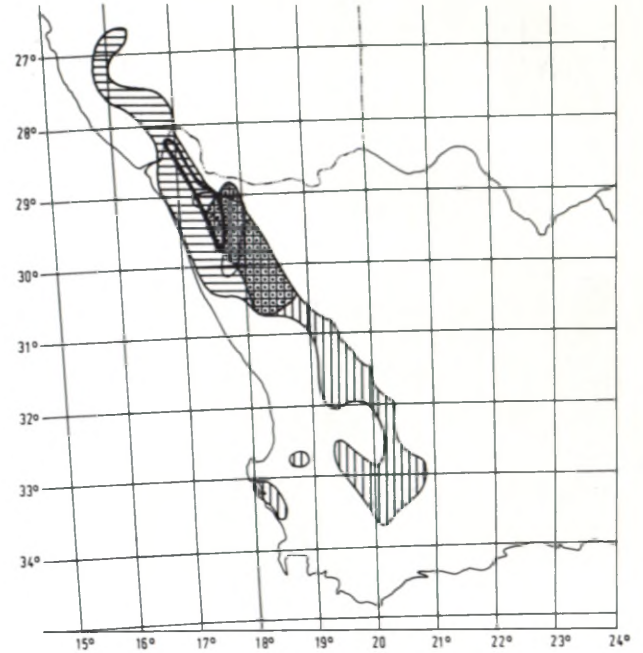

FIGURE 9. — Distribution of *Cheiridopsis* and *Odontophorus* (thin contour between latitude 28°55′ and 30°10′). Horizontal lines = *C.* subgenus *Aequifoliae;* vertical lines = *C.* subgenus *Cheiridopsis;* dots = area in which subgenera *Aequifoliae* and *Cheiridopsis* overlap; bold contour = *C.* subgenus *Odontophoroides*.
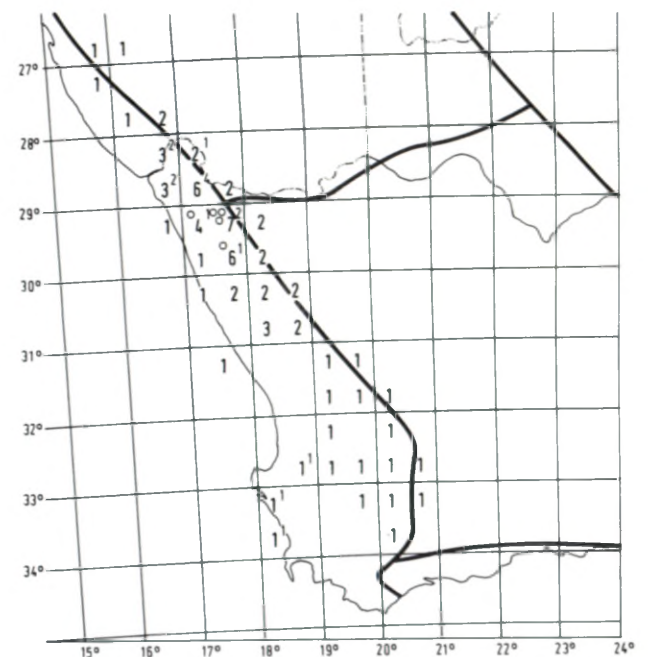

FIGURE 10. — Frequency of species of *Cheiridopsis* per 30′ × 30′ square (N = 23). Small figures indicate number of endemic species; O = *Odontophorus;* one symbol represents one species per square.

9) with an intervening zone in which they overlap. The third, smaller, subgenus *Odontophoroides,* as well as all species of the closely related genus *Odontophorus,* also occur in and near this area of overlap. Consequently the number of species per 30′ square is high (Figure 10) and contributes substantially to the formation of the southern Gariep centre (Figure 4). Furthermore, most of the endemic species of *Cheiridopsis* (occurring in at most three adjacent 30′ squares) are found here (Figure 10).

In and around the Gariep centre, sympatry of different species of *Cheiridopsis* is frequent, but in most localities different, well defined microhabitats are colonized (Hartmann & Dehn 1987). The three species of *Odontophorus* occur allopatrically in disjunct areas (Hartmann 1976) as do the six species of subgenus *Odontophoroides* (Hartmann & Dehn 1987).

Cheiridopsis and *Odontophorus* constitute a genus pair similar in principle to *Cephalophyllum/Argyroderma* in so far as the genus of restricted distribution occurs in a centre of high species frequency of the widespread genus, but they differ in so far as *Cheiridopsis/Odontophorus* only possess one centre of diversity.

Another characteristic of the *Cheiridopsis/Odontophorus* complex is its nearly exclusive distribution along the eastern boundary of the area of the subtribe at altitudes above 300 m. Only three species, *C. brownii* Schick & Tischer and *C. robusta* (Haw.) N.E. Br. in the north and *C. rostrata* (L.) N.E. Br. in the south, occur on lower coastal plains. Nevertheless, the ecological amplitude of the genus is considerable. It occurs in eight veldtypes of Acocks (1975), with one species, *C. cigarettifera* (Berger) N.E. Br. in the south, growing in six different vegetation types (Hartmann & Dehn 1987). The adaptation to shrubby Renosterveld is particularly remarkable since this vegetation type is rather remote from Karoo types of vegetation.

Jordaaniella and *Fenestraria*

A distribution pattern different from the aforementioned ones is found in the genera *Jordaaniella* H. E. K. Hartm. and *Fenestraria* N.E. Br. (Figure 11), which are distinguished from the other genera of the subtribe by a considerable reduction of the closing body (Hartmann 1982, 1983c, 1984).

The plants grow exclusively on littoral aeolian sands, the distribution coinciding with Strandveld (sensu Acocks 1975) in the coastal fogbelt (sensu Nagel 1962) along the west coast. The occurrence along the south coast agrees well with the 'south coast Strandveld' as delineated by Moll *et al.* (1984), although the easternmost population exceeds these boundaries (Figure 11).

Only five species are recognized in the complex: one in *Fenestraria* and four in *Jordaaniella* (Figure 11). Sympatry is restricted to a section along the west coast (28°–30°30′S) with a maximum of three species near 30°S, 17°E. Both endemic species *(J. clavifolia* (L. Bol.) H. E. K. Hartm. and *J. longifolia*

(L. Bol.) H. E. K. Hartm.) occur in this region, but it is doubtful whether the centre of origin lies here (Hartmann 1984).

Clearly, the limited distribution areas of both genera are due to their very narrow ecological amplitudes leaving limited scope for speciation (Hartmann 1984).
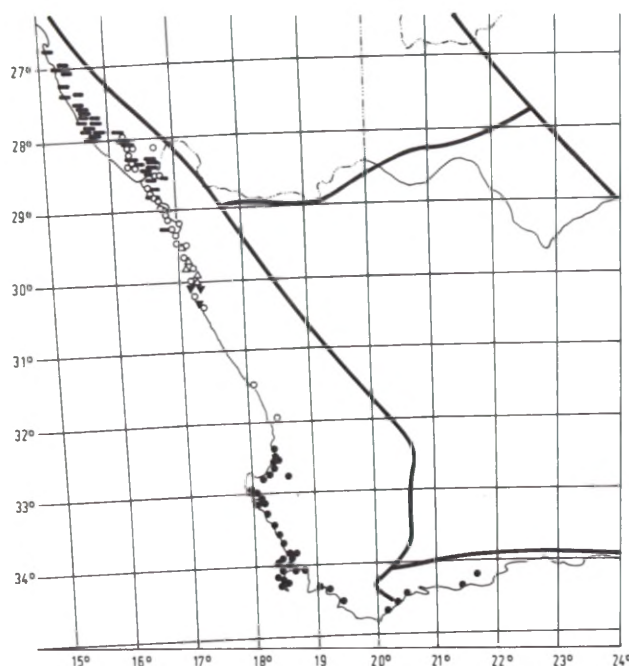

FIGURE 11. — Distribution of *Fenestraria* (solid bars) and *Jordaaniella* (open circles = *J. cuprea;* open triangles = *J. clavifolia;* full triangles = *J. longifolia;* full dots = *J. dubia).*

DISCUSSION

Interpretation of the phytogeographical data will concentrate on two different aspects: firstly the composition, development and meaning of the two geographical centres, and secondly the distribution of the genera and their possible evolution. In the process, ideas will be developed on the origin and the history of the Leipoldtiinae as a whole.

High species numbers in restricted geographical areas mostly reflect wide ecological diversity, and two processes can be distinguished: 1, specialization *in situ,* which can be recognized by a high percentage of endemic taxa; 2, overlapping of distribution areas of species which have their main (mostly wide) extension outside the centre of diversity; in the centre itself they colonize the ecologically and/or geographically extreme habitats to which they are adapted.

In the first case close relationship between the taxa is common, whereas in the second, relationship is irrelevant, the effect being simply accumulative. In both centres of multiplicity of the Leipoldtiinae, a core of closely related species, including several endemics, is found (Figures 2, 5–11). In the Gariep centre, the genera *Cephalophyllum* (Figure 6) and *Cheiridopsis* (Figure 10) represent the major portion (60–70%) of the occurring species. In the Vanrhynsdorp centre, species of *Cephalophyllum* (Figure 6)

and *Argyroderma* (Figure 5) contribute largely to the formation of the centre (up to 14 out of 17 species in one 30′ square). Of the additional taxa occurring in these centres, some clearly reach the limit of their distribution here: *Vanzijlia* and *Hallianthus* in the Vanrhynsdorp centre (Figure 8); and *Hallianthus* (Figure 8), *Jordaaniella* and *Fenestraria* (Figure 11) in the Gariep centre.

Obviously, in both centres speciation and overlapping of distribution areas contribute to the high degree of diversity, and it can be suggested that several subsequent events contributed to bring about the present situation. A similar case has been reported in the eastern Cape, for which Gibbs Russell & Robinson (1981) stress the accumulative effect of different phytochoria meeting, whereas Cowling (1982) points out certain groups with high endemism.

Both centres of the Leipoldtiinae exhibit extreme variation in geology and soils, often in island pattern distribution, a condition considered favourable for speciation of semi-isolated populations. In addition, the dense mosaic of different ecological niches in both centres permits short-distance migration under changing climatic conditions, thus allowing persistence of taxa within the area.

Consequently, it is not surprising that both phytogeographical centres have been traced in other groups as well (e.g. Nordenstam (1969) who named the Vanrhynsdorp centre, and circumscribed a 'Gariep centre' in the north). Of the two, the less prominent Vanrhynsdorp centre seems the more uniform, its undulating surface suggesting differentiation mainly in edaphic factors (e.g. Nordenstam 1969). Yet, on close investigation a wealth of ecological niches is found and is reflected in the vegetation (Jürgens 1986).

The Gariep centre has been accepted more readily as a phytogeographical centre because its geological differentiation is complimented by a large relief formation into which the extensions of the surrounding widespread plains reach (e.g. Tölken pers. comm.; Nordenstam 1969; Goldblatt 1976; Moffett 1979). The Gariep centre of the Leipoldtiinae covers a wider area (Figures 3 & 4) than the one circumscribed by Nordenstam (1969) and receives varying amounts of annual precipitation. It is not surprising, therefore, that not a single species occurs over the entire range. Distinct subcentres of genera can be seen: In *Cephalophyllum* (Figure 6), species numbers decrease from northwest to southeast, in *Cheiridopsis* (Figure 10) an increase occurs in the same direction, and *Leipoldtia* has its highest species frequency in the two central 30′ squares (Figure 8). Yet, it seems impossible to subdivide the centre into smaller entities, and it seems possible that within the area migration movements could have taken place.

Six species of five genera occur in both phytogeographical centres: *Cephalophyllum inaequale* L. Bol., *Cephalophyllum pillansii* L. Bol., *Hallianthus planus* (L. Bol.) H. E. K. Hartm., *Jordaaniella cuprea* (L. Bol.) H. E. K. Hartm., *Leipoldtia schultzei* (Schltr. & Diels) Friedrich and *Vanzijlia annulata* (Berger) L. Bol. As can be expected, all of them have their main distribution areas outside the centres, thus contributing to the 'overlapping effect' (see above).

All nine genera have different distribution patterns, and three main types can be distinguished: A — restricted distribution, B — wide distribution with one distinct centre, C — wide distribution without a distinct centre.

The genera *Argyroderma* (Figure 5) and *Odontophorus* (Figure 9) represent examples of pattern A and their restricted geographical occurrence is correlated with marked ecological adaptations (Hartmann 1976, 1978a).

Edaphic factors seem to play important roles in both genera, indicating that speciation may have occurred in the present areas of distribution. This would suggest that appropriate climatic conditions have prevailed for a considerable period allowing extensive radiation processes to take place.

A genus of wide distribution with one distinct centre of diversity (pattern B) is *Cheiridopsis,* where highest species numbers and occurrence of all three subgenera coincide (Figures 9 & 10). Based mainly on morphological data, Hartmann & Dehn (1987) suggest that the centre of origin of the genus (and of the closely related genus *Odontophorus)* lies here, speciation having been promoted by the varied ecological conditions within the southern Gariep centre (see above). Marginal speciation (via semi-isolated populations) in extreme habitats seems to have been rare and has been recorded for *Cheiridopsis carolischmidtii* (Dinter & Berger) N.E. Br. in the north on weathered gneiss in the March rainfall area, and *Cheiridopsis rostrata* (L.) N.E. Br. in the south-west on sandy soils in West Coast Strandveld (sensu Moll et al. 1984). *Leipoldtia* can be taken as another example of distribution pattern B, but the centre is less prominent and marginal speciation (Figure 8) more frequent — both smaller subgenera colonize the border areas. The genus could therefore also be seen as an example of pattern C, which lacks a distinct centre. The predominantly shrubby habit and generally low expression of succulence in leaf, stem and root indicate that *Leipoldtia* may have evolved under slightly wetter conditions than it experiences today, perhaps even outside its present distribution area.

The widespread monotypic genera *Fenestraria* (Figure 11), *Hallianthus* and *Vanzijlia* (Figure 8) naturally lack centres of species richness, and even surveys for character multiplicity (Hartmann 1982, 1983a, 1983b) have not yielded positive results. Differentiation patterns can be correlated with geographical distribution (flower characters in *Fenestraria,* Hartmann 1982) or ecological factors (germination in *Vanzijlia,* Hartmann 1983a) or they can occur incidentally (flower characters in *Hallianthus* with island-type distribution, Hartmann 1983b). Adaptation to rocky habitats restricts the distribution of *Hallianthus*. The genus could well have occurred over wider conjunct areas at a time when sedimentary plains covered less ground.

Assessment of the widespread genus *Jordaaniella* is complicated by the strict adaptation to coastal habitats (Figure 11) over several climatic ranges. Ex-

tensive migration along the coast could have taken place, and although three of the four species occur in close proximity (near 30°S, 17°E, Figure 11) it does not seem justified to conclude that this region is the centre of origin (see also Hartmann 1984). Nevertheless, the creeping habit and prolonged germination indicate that the genus probably originated in a coastal habitat.

The large genus *Cephalophyllum* exhibits a complex distribution pattern which cannot be assigned to one of the types mentioned above. Following the character analyses of Hartmann (1978b, in press), the most primitive capsule types and least specialized growth forms occur in species in the Vanrhynsdorp centre, where the highest species frequencies of the genus are found as well (Figure 6). But the number of endemics is low, suggesting that the present species richness is mainly due to overlapping of distribution areas.

In contrast, the species of the Gariep centre show a high degree of uniformity in capsule morphology, differing mainly in habitat and seed characters, so that this region can be considered to represent a centre of origin for part of the genus (Hartmann in press).

In contrast to *Cheiridopsis* (above), relations between the two subgenera cannot be elucidated from distribution data alone (Figure 2). This is mainly due to the more or less strict allopatric occurrence of the nine species of *Cephalophyllum* subgenus *Cephalophyllum*, in which highest frequencies per 30' square (three species, Hartmann in press) are attained mainly by overlapping of wide distribution areas (only two species of restricted distribution are known, one of them isolated in the south-west, see Figure 6). Speciation in this subgenus seems to have followed predominantly the parapatric model (sensu Wiley 1981) in which narrow contact zones existed between diverging populations.

Some speculations can be made on the phytogeographical development of *Cephalophyllum*. The predecessor of this genus (and *Argyroderma?*) could have existed in the Vanrhynsdorp centre, but a major part of the genus would have occurred in (or migrated to ?) adjacent areas. Differentiation of the two subgenera possibly took place outside the present distribution range, probably followed by a phase of extensive geographical spreading — *Cephalophyllum* subgenus *Cephalophyllum* mainly into the wetter south, subgenus *Homophyllum* mainly into the drier north of the present distribution area. While parapatric speciation may have prevailed in subgenus *Cephalophyllum*, radiation of a considerable part of the subgenus *Homophyllum* could have taken place in the Gariep centre. Distribution pattern B (above) can be applied to this species group.

At first sight it seems improbable that a common pattern for the biogeographical development of the Leipoldtiinae can be found. But the extensive meshing of character states, as demonstrated for the subtribe by Hartmann (1983c), clearly indicates that it constitutes a monophyletic group. The area of origin cannot be deduced from present distribution data and may well have lain outside the existing range.

Yet, it was probably not too far away because speciation processes are generally slow and many taxa of restricted occurrence (e.g. species of *Cheiridopsis* subgenus *Odontophoroides*) and/or with narrow ecological amplitude (e.g. *Argyroderma, Fenestraria*) can hardly be imagined to have migrated far.

With respect to ecology, the present data suggest that a winter rainfall regime with rather low annual amounts of precipitation (<200 mm, Figure 5) could have prevailed in the area of origin. The few extant exceptions could be seen as ecological fugitives. It is difficult though to localize an adequate region in the past, as opinions on past climates in South Africa are highly controversial (e.g. Van Zinderen Bakker Sr 1978; Deacon 1983), in particular with reference to the extent of the winter rainfall area (e.g. Van Zinderen Bakker Sr 1976, 1978; Lancaster 1979) in the late Pleistocene. In any case, it is accepted that higher precipitation prevailed in the west than at present (Kent & Griebnitz 1985). This leads some authors to the conclusion that the Namib is of rather recent origin (e.g. Tankard & Rogers 1978; Axelrod & Raven 1978) while others (e.g. Lancaster 1979) assume that arid 'isolated refuges along the Namib coast' or widespread deserts (e.g. Sarnthein 1978) existed during the wet phases of the late Pleistocene. Van Zinderen Bakker Sr (1978) also states that the Namib is 'ancient' and has only marginally been influenced by higher rainfall, retaining its 'hyper-arid centre' since the late Tertiary. An area like this could present an ideal cradle for speciation, permitting successive peripheral isolation of populations while re-migration could occur as well.

It seems possible therefore, that the predecessors of the extant genera of Leipoldtiinae originated on the fringes of an ancient Namib, probably under slightly higher rainfall regimes than today (based on the assumption that the less pronounced xeromorphic character expressions in *Leipoldtia, Cephalophyllum* and *Jordaaniella* reflect the more primitive stages). The existence of strictly coastal taxa *(Jordaaniella, Fenestraria)* suggests that similar habitats were already available during early speciation processes.

The origin of the Leipoldtiinae as a whole remains even more obscure than the diversification within the subtribe. By its unique morphological character set, the taxon is rather isolated within the family, although the xeromorphic leaf characters indicate that the closest relatives must be sought among the xeromorphic genera of the subfamily Ruschioideae. The main frequency centre of these genera lies around the mouth of the Orange River, coinciding with the Gariep centre of the Leipoldtiinae. A less pronounced centre is found in the Little Karoo, and a third minor one in the Knersvlakte (Vanrhynsdorp centre), but genera of xeromorphic Ruschioideae occur as far east at 29°E, and as far north as 26°S in almost every degree square. Leipoldtiinae colonize a restricted area within the range of the Ruschioideae, thus emphasizing the relative isolation of the group. They contribute substantially to the formation of the western frequency centres (up to 50% of genera per 30' square), and present a typical 'arid winter rainfall' distribution.

The possibility cannot be excluded that this climatic regime presents the centre of origin of the xeromorphic members of the Ruschioideae, but in the absence of information from less derived subtribes no evidence can be offered for or against the suggestion.

With reference to the entire family, it may be important to note that distribution patterns of both subfamilies coincide almost completely, and that non-xeromorphic genera have their centres of frequency in the winter rainfall region as well. It can therefore be suspected that adaptation to winter rainfall with lower precipitation amounts could present a primary step of evolution within Mesembryanthemaceae, but the phytogeography of the Leipoldtiinae cannot be used as proof because of their specialized derived character set.

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