

# CLADISTIC BIOGEOGRAPHY IN THE ATLANTIC ISLANDS: A CASE STUDY BASED ON TWO PLANT GENERA, *LOBULARIA* AND *NAUPLIUS*

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With 6 figures and 2 appendixes

*ABSTRACT.* Area cladograms based on cladistic analyses of two genera of flowering plants, *Lobularia*, Brassicaceae, and *Nauplius*, Asteraceae, were compared. These genera have three areas of endemism in common: (1) The continental eastern Canary Islands, i. e. Lanzarote and Fuerteventura, and the "Macaronesian" enclave in Morocco; (2) The oceanic, central and western Canary Islands; and (3) The Cape Verde Islands. The reduced area cladograms for these three areas were more or less identical for the two genera. The first area, the continental Canaries, together with the Moroccan enclave, was isolated first in both analyses and appeared as older than the oceanic Canaries and the Cape Verdes. The oceanic Canaries and the Cape Verdes seemed to have ancestral populations in common much closer in time than the continental and oceanic parts, respectively, of the Canaries. The resulting hypothesis of a closer biogeographical connection between the oceanic Canaries and the Cape Verdes than within the Canaries is discussed in relation to vicariance and dispersal biogeography.

Cladistic biogeography is an analytical, historical biogeography which combines vicariance biogeography with ideas from CROIZAT'S (1958, 1964) non-phylogenetic theory of "panbiogeography" and "generalized tracks" and area relationships based on the cladistic principles of HENNIG (1950, 1966), as first applied by BRUNDIN (1966, 1972a, 1972b) and later developed by ROSEN (1976, 1978), PLATNICK & NELSON (1978), NELSON & PLATNICK (1981), and HUMPHRIES & PARENTI (1986).

The method is based on two main criteria: (1) cladistic analyses of at least two

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unrelated groups of organisms, and (2) the occurrence of these groups in at least three common areas of endemism. WICKLUND (1987) presented a cladistic analysis of the composite genus *Nauplius* Cass., while I here present the results of a similar analysis of the crucifer genus *Lobularia* Desv. (see Appendixes 1-2). Thus, the first criterion is satisfied.

Both genera have a similar Mediterranean-Macaronesian distribution. The biogeographic term "Macaronesia" is here adopted after SUNDING (1979) and includes the Atlantic archipelagos of the Azores, Madeira, Salvage Islands, Canary Islands, and Cape Verde Islands plus an enclave in Morocco (Fig. 1). The Macaronesian areas which the two genera share can be defined as three areas of endemism (Fig. 1): (1) The continental, eastern Canary Islands, i. e. Lanzarote and Fuerteventura, together with the enclave in Morocco. (2) The presumably oceanic, central and western Canary Islands, i. e. Gran Canaria, Tenerife, La Gomera, La Palma, and El Hierro. (3) The Cape Verde Islands.

This subdivision reflects the geological complexity of the Canary Islands (cf. SCHMINCKE 1976) and the floristic and faunistic delimitation between the eastern Canaries and the Moroccan enclave on the one hand, and the central and western Canaries on the other. The Cape Verde Islands constitute a geographically, geologically, floristically, and faunistically well delimited area. With areas thus circumscribed, the second criterion is also satisfied.

Under a vicariance model, we must presume that ancestral populations of *Nauplius* and *Lobularia* existed across their present areas of distribution, i.e. from the Canaries and Cape Verdes in the west, across mainland Africa to the Middle East and northwards to Mediterranean Europe. Some endemic Macaronesian plant taxa of groups with such distribution patterns today, have been interpreted as descendants of the subtropical flora south of the Tethys Sea in early Tertiary some 65 Myr BP (cf. BRAMWELL 1976). Records of Tertiary fossils in southern Europe support the theory (SAPORTA 1862-1874, DEPAPE 1922, CIFERRI 1962).

### The *Nauplius* case

In her analysis of *Nauplius* (Fig. 2), with *Asteriscus* Mill. as outgroup, Wicklund (1987) used HENNIG'S (1966) method, modified by NELSON & PLATNICK (1981) and WILEY (1981), that is a strict parsimony analysis. Based on 20 characters, the analysis resulted in a most parsimonious cladogram which was 22 steps long, with two cases of homoplasy: parallelism in character 3 and reversal in character 1. Above the taxa in Fig. 2, the three areas of endemism are marked with numbers. Unmarked taxa have another, often wider, distribution. In Fig. 3, hypothetical, historical populations are denoted by letters, A-L. In Fig. 2, the contemporary taxa of *Nauplius* and its sister group *Asteriscus* are marked with

letters corresponding to those in Fig. 3.

The evolutionary process can be divided in six steps, I - VI. Step I circumscribes the hypothetical population ancestral to both *Nauplius* and *Asteriscus* (A-L, Fig. 3). In step II a chromosomal differentiation occurs, and the two sister groups, *Asteriscus* (A), with  $n=5,6$ , and *Nauplius* (B-L), with  $n=7$ , are split. An internal barrier to gene exchange is established, and the two genera coexist sympatrically today.

Step III involves the isolation of population BC in area 1, i. e. the eastern Canaries and the enclave. In step IV, population BC is split in two populations, corresponding to extant taxa: B=*N. schultzi* (Bolle) Wikl. (whole area 1) and C=*N. imbricatus* (Cav.) Wikl. (enclave only). Furthermore, two allopatric populations are isolated: D=*N. sericeus* (L. fil.) Cass. (Fuerteventura) and E=*N. intermedius* Webb in Webb et Berth. (Lanzarote). *Nauplius schultzi* occurs sympatrically with *N. intermedius* today, and parapatrically with *N. sericeus*, i. e. on the same island but in different habitats. Crossing experiments (HALVORSEN & BORGEN 1986) revealed internal barriers between *N. schultzi* and *N. intermedius*. Similar barriers may exist between the two partly sympatric sister species *N. schultzi* and *N. imbricatus*. Overlapping distributions today may be due to stochastic, historical causes, for instance dispersal.

Step V involves the isolation of the Cape Verde population, F+G+H, area 3. Also, N=*N. aquaticus* (L.) Cass. and the three subspecies of *N. graveolens* (Forssk.) Wikl., i. e. I=ssp. *stenophyllus* (Link in Buch) Wikl., J=ssp. *odorus* (Schousb.) Wikl., and K=ssp. *graveolens*, are split off. The ssp. *stenophyllus* is endemic to Gran Canaria; ssp. *odorus* occurs in NW Africa and Gran Canaria; ssp. *graveolens* throughout N Africa and the Middle East, partly sympatrically with ssp. *odorus*. The present sympatry may result from dispersal. In Gran Canaria, ssp. *stenophyllus* and *odorus* are geographically and ecologically separate except in one area of hybridization. The annual, allogam *N. aquaticus* grows sympatrically with all ssp. of *N. graveolens* but is reproductively isolated from these (HALVORSEN & BORGEN 1986).

In step VI, three populations in the Cape Verdes are isolated: N. *daltonii* (Webb) Wikl., with H=ssp. *daltonii* on Santiago and G=ssp. *vogelii* (Webb) Wikl. on all western islands (parapatric with ssp. *daltonii* on Santiago), plus F=*N. smithii* (Webb) Wikl. in a restricted area on São Nicolau.

### The *Lobularia* case

In my analysis of *Lobularia*, I used *L. maritima* (L.) Desv.,  $n=12$ , as outgroup for the analysis of the monophyletic  $n=11$  group, i. e. the widely distributed allogam, annual *L.*

*libyca* and the predominantly autogam, perennial, more or less suffruticose *L. canariensis* (DC.) BORGEN complex, with nine endemic, Macaronesian subspecies. Both a compatibility analysis (MEACHAM 1981) and a Wagner parsimony analysis (programme PHYLIP), were performed. Based on 24 characters, both methods resulted in two most parsimonious cladograms/consensus trees, each 27 steps long. One is presented in Fig. 4, with homoplasies in characters 2,4,5.

The ancestral as well as the more recent populations are denoted by letters, A-K (Figs. 4-5), and the evolutionary process is divided in six steps, I-VI, step I being the presumed ancestral *Lobularia* population. Parallel to the *Nauplius* case, step II involves chromosomal divergency, i.e. dysploidy, splitting *L. maritima* (A), n=12, from its n=11 sister group (B-K). Presumably, *L. maritima* is indigenous to the W Mediterranean region. It has been distributed as an ornamental plant to gardens all over the world, at least since 1681 (Kuijlen et al. 1983). Due to its capacity for subsequent dispersal, it now occurs as a more or less naturalized garden escape in the floras of all continents except Antarctica. It is reproductively isolated from the other species (BORGEN 1987).

In step III, four populations are isolated: one in area 1 plus the Mediterranean region (BC), one in areas 2 + 3 (DFGHI), and two (J + K) in the Salvage Islands. Parallel to *Nauplius*, step IV involves the isolation of one population, C=ssp. *marginata* (Webb) Borgen in area 1 from the more widely distributed population B=*L. libyca* (Viv.) Meisn. throughout N Africa and the Middle East, with scattered finds in S Europe, the Canaries, and Madeira. Some of the occurrences of *L. libyca* today are probably due to dispersal. *Lobularia libyca* is reproductively isolated from the other species (Borgen 1987). Furthermore, step IV results in the isolation of I=ssp. *microsperma* Borgen in the southwestern parts of Gran Canaria and Tenerife, where it occurs parapatrically with ssp. *canariensis*.

In step V, again parallel to the *Nauplius* case, one population, DE, is isolated in area 3, the Cape Verdes. Also, three populations are isolated in area 2: F=ssp. *palmensis* (Christ) Borgen on La Palma and Tenerife; G=ssp. *intermedia* (Webb) Borgen on Tenerife, La Gomera, La Palma, and El Hierro; and H=ssp. *canariensis* on Gran Canaria and Tenerife. The present occurrences of ssp. *intermedia* on La Palma are few and probably due to dispersal. The ssp. *intermedia* and *canariensis* occur parapatrically on Tenerife.

Similar to the *Nauplius* case, the last step (VI) involves the splitting of the Cape Verde population. Taxon D= ssp. *fruticosa* (Webb) Borgen is found on all western islands except São Vicente. Taxon E=ssp. *spathulata* (J. A. Schmidt) Borgen has its main distribution on São Vicente, but a slightly deviating and possibly secondary population occurs on São Nicolau, at a distance from those of ssp. *fruticosa*.

### Biogeographical interpretations

The biogeographical implications of the two cladograms can be viewed both in a vicariance and a dispersal context (cf. BREMER 1992), even though cladistic biogeography by definition views the historical events from a vicariance perspective only. Most important is that the two cladograms (Figs. 2 and 4) are congruent on essential points: (1) In both genera, populations in area 1, i. e. the eastern, continental Canaries and the Moroccan enclave, are isolated first and, notably, before the populations in the oceanic, central and western Canaries are split off from those in the Cape Verdes. Under a vicariance model, this means, if the cladistics are correct, that area 1 is older than areas 2 and 3. (2) The Cape Verde populations are, in both cases, isolated remarkably late from those in the oceanic Canaries. If the cladistics are correct, this implies that in both genera, the populations in the oceanic Canaries have a more recent ancestor in common with populations in the Cape Verdes than with populations in the continental Canaries. (3) In both genera, the last event is the isolation of the populations within the archipelago of Cape Verde.

By replacing taxa with areas and only including areas of endemism in common, a reduced area cladogram, more or less identical for both genera, is constructed (Fig. 6). Under a vicariance model, a continuous area 1 + 2 + 3 has first been split in two areas, 1 and 2 + 3. Next, area 2 + 3 is split in separate areas, 2 and 3. *Lobularia* apparently deviates slightly from *Nauplius* by splitting off area 2 twice.

Several hypotheses have been put forward on the origin of the Macaronesian archipelagos (see EVERS et al. 1970, and Sunding 1979): (1) "The Oceanic Island Theory" implies that all islands are a result of oceanic volcanism, that started as submarine eruptions. (2) "The Land Bridge Theory" holds that the islands are oceanic, but have been larger in the past and more or less connected with each other and possibly also with the mainland. (3) "The Fragmentation Theory" claims that the islands have loosened as fragments of the Old World's continental edges. (4) "The Atlantis Theory" also holds that the islands are fragments, not of the continent but of a greater landmass situated between Africa and America and possibly connecting the two continents. Of these hypotheses, (1) and (2) are consistent with dispersal; (3) and (4) with vicariance.

The fourth hypothesis is abandoned due to lack of evidence (cf. SUNDING 1979). As for the others, it is commonly accepted today that at least Lanzarote and Fuerteventura are of continental origin (cf. SCHMINCKE 1976). These islands were probably separated from the African mainland in Upper Cretaceous, dated to 80-100 Myr BP (cf. ROTHE 1968, RAVEN & AXELROD 1974). The volcanic activity on the other Canary Islands seems rather recent, dated to Miocene/Oligocene in mid Tertiary, ca. 35 Myr BP (SCHMINCKE 1976). The oceanic depths between the western Canaries are up to 3000 m and at least La Palma, El Hierro, and

La Gomera appear to lie on an oceanic crust (DASH & BOSSHARD 1969). Thus the Canaries could be a "composite archipelago" (cf. AXELROD 1960, SUNDING 1979), with some islands being continental and others oceanic in origin. If so, the three first hypotheses may all represent some truth and the observed biogeographical patterns may have resulted from a combination of vicariance and dispersal events.

Being situated 500 km off the African mainland and surrounded by ocean depths of 4000 m or more, the Cape Verdean archipelago is usually regarded as truly oceanic in origin. Among a few contradictory facts are the occurrence of limestone rocks of Jurassic age on the island of Maio (KREJCI-GRAF 1961, KLERKX & DE PAEPE 1971). These rocks are the oldest in whole Macaronesia. Besides, 11 % of the flora (SUNDING 1979) and a substantial part of the fauna are Macaronesian, despite a distance of 1400 km to the Canaries.

Neither *Lobularia* nor *Nauplius* are particularly well adapted to dispersal but light seeds, combined with a slight seed wing in *Lobularia*, and small pappus scales on the achenes of *Nauplius* might aid wind dispersal. The prevailing wind direction favours dispersal from the mainland to the archipelagos, not between the archipelagos. Increased distance also makes dispersal between the two archipelagos unlikely. Thus wind, particularly storms, may operate as a dispersal agent from the African continent to the Canarian and Cape Verdean archipelagos and also locally within and between islands of each archipelago.

It is tempting to postulate an ancestral area (center of origin/dispersal) in the African mainland as the source area for small, isolated populations in the Atlantic islands of Macaronesia. As a consequence of the founder effect, the evolution in the islands may have occurred according to the Quantum speciation model outlined by GRANT (1971, 1981), with selection and drift operating simultaneously, resulting in a more or less punctualistic speciation.

The close cladistic relationship between taxa in the oceanic Canaries and the Cape Verdes indicates common ancestry. In both genera, the ancestors could have belonged to mainland populations of the Tertiary flora south of the Tethys Sea. With fairly short distances to the source area and favourable wind directions, a dispersal model, with barriers and areas of older age than the taxa, could explain the pattern indicated for areas 2 and 3 in the reduced area cladogram.

The combined cladistic patterns for the two genera, *Nauplius* and *Lobularia*, indicate that area 1, i. e. Lanzarote + Fuerteventura + the Moroccan enclave, is older than areas 2 and 3. Presumably, in area 1 the barriers are secondary and speciation have followed a strict vicariance model, with barriers and taxa of the same age, the barriers fragmenting the former

larger ranges of ancestral taxa. For the other areas, dispersal and vicariance patterns cannot be resolved decisively but basic geological information, i. e. the oceanic island theory, favours a dispersal model. Thus, a combination of vicariance and dispersal phenomena may best explain the biogeographical patterns revealed by this cladistic approach.

Two cladograms represent the minimum for performing a cladistic biogeographical analysis. Besides, the two cladograms are not fully resolved and biogeography is never better than the taxonomy on which it is based. It seems, however, from this case study that more cladistic analyses could contribute to further insight in biogeographical patterns and pathways in the Atlantic Islands of Macaronesia. Apparently, the particular patterns presented here seem to conform to a more general pattern caused by the same set of historical events. Even though stochastic historical events like dispersal and extinction may blur the observed patterns to some extent, resolution of patterns seem promising with a cladistic approach.

## REFERENCES

AXELROD, D. I.:

1960. The evolution of flowering plants. - In S. Tax (ed.), *Evolution after Darwin, I*, Univ. Chicago Press, Illinois, pp. 227-307.

BORGEN, L.:

1987. *Lobularia* (Cruciferae). A biosystematic study with special reference to the Macaronesian region. - *Opera Botanica* 91: 1-96.

BRAMWELL, D.:

1976. The endemic flora of the Canary Islands. Distribution, relationships and phytogeography. - In G. Kunkel (ed.), *Biogeography and Ecology in the Canary Islands*, W. Junk B. V., The Hague, pp. 207-240.

BREMER, K.:

1992. Ancestral areas: a cladistic reinterpretation of the center of origin concept. - *Syst. Biol.* 41: 436-445.

BRUNDIN, L.:

1966. Transantarctic relationships and their significance as evidenced by midges. - *Kungl. Svenska Vet. akad. Handl., Ser. 4*, 11:1-472.
- 1972a. Evolution, causal biology, and classification. - *Zool. Scripta* 1:107-120.
- 1972b. Phylogenetics and biogeography. - *Syst. Zool.* 21:69-79.

CIFERRI, R.:

1962. La Laurisilva Canaria: una paleoflora vivente. - *Ricerca Scient.* 32(1): 111-134.

CROIZAT, L.:

1958. *Panbiogeography*. - Published by the author, Caracas.
1964. *Space, time and form, the biological synthesis*. - Published by the author, Caracas.

DASH, B. P. & BOSSHARD, E.:

1969. Seismic and gravity investigations around the western Canary Islands. - *Earth Planet. Sci. Lett.* 7: 169-177.



DEPAPE, G.:

1922. Recherches sur la flore pliocène de la Vallée du Rhone. - *Ann. Sci. nat., Bot. ser. 10, 4*: 73-265.

EVERS, A., KLEMMER, K., MÜLLER-LIEBENAU, I., OHM, P., REMANE, P., STRASSEN, R. ZUR & STURHAN, D.:

1970. Erforschung der mittelatlantischen Inseln. - *Umsch. Wissensch. Techn. 70*: 170-176.

GRANT, V.:

1971. *Plant Speciation*. - Columbia Univ. Press, New York.  
1981. *Plant Speciation, 2nd ed.* - Columbia Univ. Press, New York.

HALVORSEN, T. & BORGES, L.:

1986. The perennial Macaronesian species of *Bubonium* (Compositae - Inuleae). - *Sommerfeltia 3*: 1-103.

HENNIG, W.:

1950. *Grundzüge einer Theorie der phylogenetischen Systematik*. - Deutscher Zentralverlag, Berlin.  
1966. *Phylogenetic Systematics*. - Univ. of Illinois Press, Urbana.

HUMPHRIES, C. J. & PARENTI, L. R.:

1986. Cladistic Biogeography. - *Oxford Monographs on Biogeography No. 2*, Clarendon Press, Oxford.

KLERKX, J. & DE PAEPE, P.:

1971. Cape Verde Islands: Evidence for a Mesozoic oceanic ridge. - *Nature, Lond.* 233: 117-118.

KREJCI-GRAF, K.:

1961. Vertikal-Bewegungen der Makaronesen. - *Geol. Rundschau 51*: 73-122.

KUIJLEN, J., OLDENBURGER-EBERS, C. S., & WIJNANDS, D. O.:

1983. *Paradisus Batavus. Bibliografie van planten-catalogi van onderwijstuinen, particuliere tuinen en Kwekerscollecties in de Noordelijke en Zuidelijke Nederlanden (1550-1839)*. - Pudoc, Wageningen.

MEACHAM, C.:

1981. A manual method for character compatibility analysis. - *Taxon 30*: 591-600.

NELSON, G. & PLATNICK, N.I.:

1981. *Systematics and biogeography: cladistics and vicariance*. - Columbia Univ. Press, New York.

PLATNICK, N. I. & NELSON, G.:

1978. A method of analysis for historical biogeography. - *Syst. Zool.* 27: 1-16.

RAVEN, P. H. & AXELROD, D. I.:

1974. Angiosperm biogeography and past continental movements. - *Ann. Miss. Bot. Garden* 61: 539-673.

ROSEN, D. E.

1976. A vicariance model of Caribbean biogeography. - *Syst. Zool.* 24: 431-464.  
1978. Vicariant patterns and historical explanations in biogeography. - *Syst. Zool.* 27: 159-188.

ROTHER, P.:

1968. Mesozoische Flysch-Ablagerungen auf der Kanareninsel Fuerteventura. - *Geol. Rundschau* 58: 314-332.

SAPORTA, G. DE.:

- 1862-1874. Études sur la Végétation du sud-est de la France à l'époque tertiaire. - *Ann. Sci. Nat. Bot. Sér. 4*, 16: 309, 348, 17: 191-311 (1862), and 19: 5-124 (1863). *Sér. 5*, 3: 5-152 (1865), 8: 5-136 (1867), 9: 5-62 (1868), 15: 277-351 (1872), 17: 5-44 (1873), and 18: 23-146 (1874).

SCHMINCKE, H.-U.:

1976. The geology of the Canary Islands. - In G. Kunkel (ed.), *Biogeography and Ecology in the Canary Islands*, W. Junk B. W., The Hague, pp. 67-184.

SUNDING, P.:

1979. Origins of the Macaronesian flora. - In D. Bramwell (ed.), *Plants and Islands*, Academic Press, London, New York, Toronto, Sydney, San Francisco, pp. 13-40.

WIKLUND, A.:

1987. The genus *Nauplius* (Asteraceae - Inuleae). - *Nord. J. Bot.* 7: 1-23.

WILEY, E. O.:

1981. *Phylogenetics: the theory and practice of phylogenetic systematics*. - John Wiley and Sons, New York.

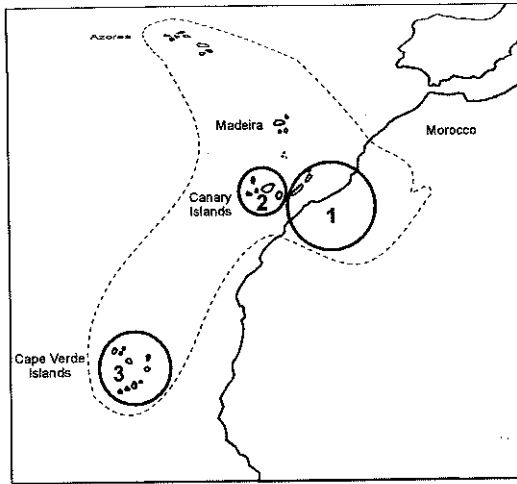


Figure 1 - Areas of endemism in common to *Lobularia* and *Nauplius* (circles) within the biogeographical region of Macaronesia (broken line).

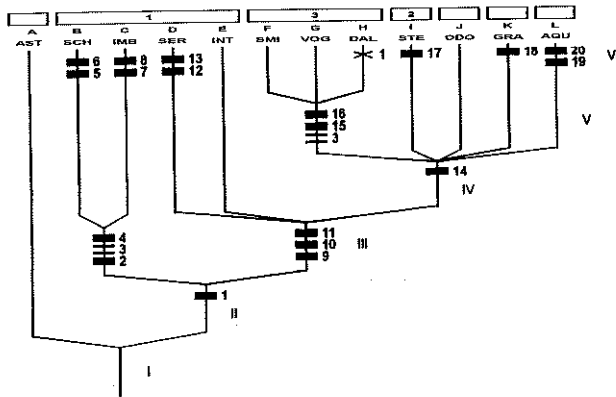


Figure 2 - Cladogram for *Nauplius*, modified after Wicklund (1987). A= *Asteriscus* (outgroup), B=*Nauplius schultzei*, C=*N. imbricatus*, D=*N. sericeus*, E=*N. intermedius*, F=*N. schmithii*, G=*N. daltonii* ssp. *vogelii*, H=*N. daltonii* ssp. *daltonii*, I=*N. graveolens* ssp. *stenophyllus*, J=*N. graveolens* ssp. *odoratus*, K=*N. graveolens* ssp. *graveolens*, L=*N. aquaticus*. Areas of endemism marked above taxa. Evolutionary steps denoted I-VI.

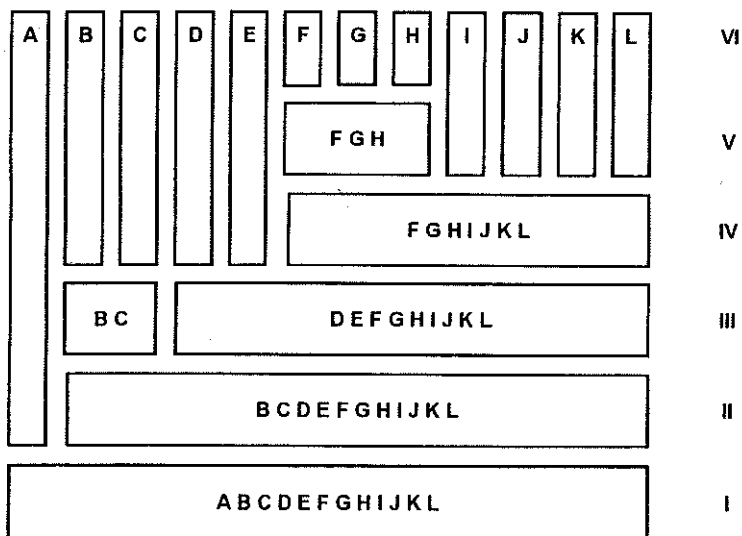


Figure 3 - Schematic drawing of hypothetical, historical populations, A-L, and vicariance events, steps I-VI, in *Nauplius* and its sister group, *Asteriscus*.

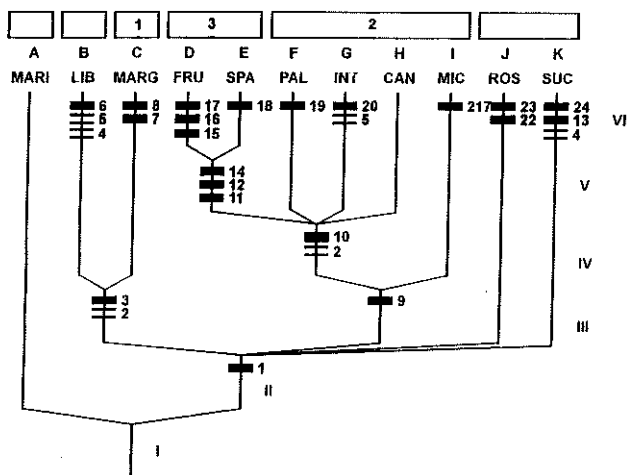


Figure 4 - Cladogram for the genus *Lobularia* (unpublished). A=*L. maritima* (outgroup), B=*L. libyca*, C-K=*L. canariensis*; C=*ssp. marginata*, D=*ssp. fruticosa*, E=*ssp. spathulata*, F=*ssp. palmensis*, G=*ssp. intermedia*, H=*ssp. canariensis*, I=*ssp. microsperma*, J=*ssp. rosula-venti*, K=*ssp. succulenta*. Areas of endemism marked above taxa. Evolutionary steps denoted I-VI.

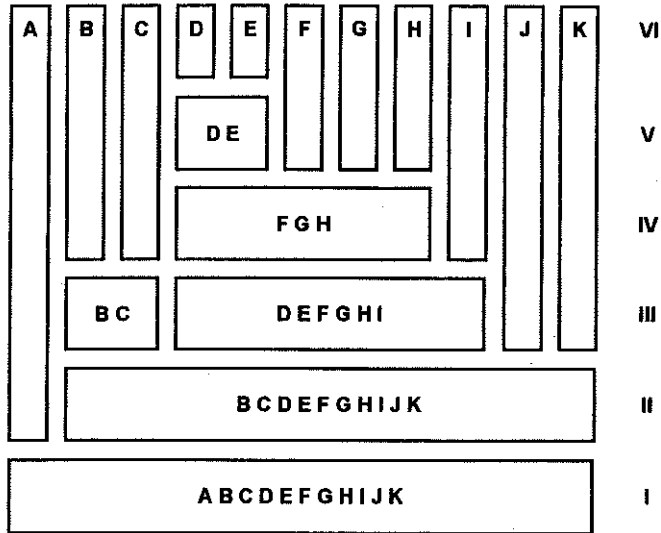


Figure 5 - Schematic drawing of hypothetical, historical populations, A-K, and vicariance events, steps I-VI, in *Lobularia*.

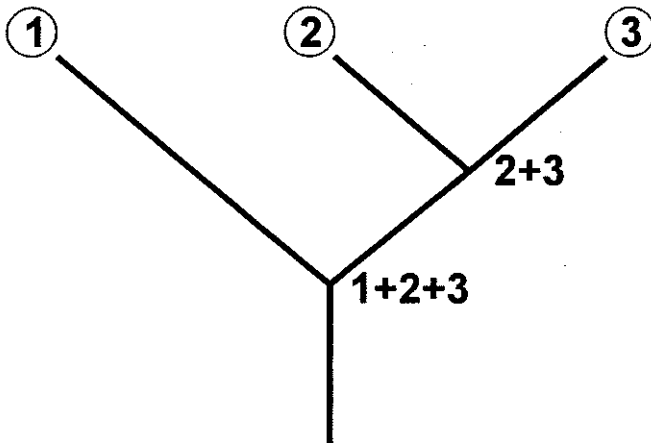


Figure 6 - Reduced area cladogram representing *Nauplius* and *Lobularia*.

**APPENDIX 1** - Character states in *Lobularia*. The numbers correspond to the numbers in the matrix (Appendix 2), and in the cladogram (Fig. 4).

**Plesiomorphic**

1. One seed per locule
2. Seeds terete, wingless
3. Silicle valves convex, smooth
4. Life form perennial
5. Petals more than 1.2 mm wide, width claw and blade
6. Pedicels longer than the silicles
7. Silicle margin thin, smooth
8. Silicles longer than wide, with less than 3 mm
9. Flowering raceme dense, many-flowered, flowers overtopping buds
10. Plants branched from the base, woodiness slight
11. Leaves greyish-silvery pubescent
12. Leaves narrow, less than 3 mm wide
13. Leaves not obtrullate
14. Leaf base cuneate
15. Bark light greyish brown
16. Leaves one-nerved
17. Leaf margin entire
18. Habit ascending, stiff
19. Leaves ascending, straight, length: width ratio less than 16
20. Petals white, ascending, margins straight
21. Seeds suborbicular, more than 1 mm wide
22. Leaves alternate
23. Fruiting raceme elongate, more than 2.5 cm long
24. Leaf succulence absent or slight

**Apomorphic**

1. More than one seed per locule
2. Seeds half-terete, winged
3. Silicle valves flat, bulging
4. Life form annual
5. Petals narrow, less than 1.2 mm wide, spatulate
6. Pedicels shorter than the silicles
7. Silicle margin thick, twisted
8. Silicles almost as wide as long, width more than 3 mm
9. Flowering raceme open, few-flowered, buds overtopping flowers
10. Plants branched from a stem, woodiness pronounced
11. Leaves subglabrous
12. Leaves broad, 4-8(-16) mm wide
13. Leaves obtrullate
14. Leaf base attenuate
15. Bark dark red-brown
16. Leaves with forked nerves
17. Leaf margin crenulate
18. Habit pendulous, lax
19. Leaves declinate, lax, length: width ratio more than 16
20. Petals creamy, horizontally spreading, margins recurved
21. Seeds oblong, less than 1 mm wide
22. Leaves clustered
23. Fruiting raceme condensed, less than 2.5 cm long
24. Leaf succulence pronounced

