

BIOGEOGRAFIA HISTÓRICA

ENFOQUES FUNDAMENTAIS

Dispersalismo – Darwin 1859, Wallace 1876

Biogeografia filogenética – Hennig 1966, Brundin 1966

Áreas ancestrais – Bremer 1992, Ronquist 1994

Panbiogeografia – Croizat 1958, Craw 1988, Page 1987

Biogeografia cladística – Nelson 1974, D. Rosen 1976, Nelson & Platnick 1981

Análise de parcimônia de endemismos (PAE) - B. Rosen 1988, Craw 1988, Morrone 1988

Métodos baseados em eventos – Page 1994, Ronquist 1997

Filogeografia – *Avise et al.* 1987

Biogeografia experimental – Haydon, Tadtkey & Pianka 1994

Biogeografia Integrativa – Donoghue & Moore 2003

Box 7.1 Donn Eric Rosen (1929–1986)



Donn Rosen

Figure 7.1. Donn Rosen in his office and lab at the American Museum of Natural History. [Photograph courtesy of the late Carmela B. Rosen.]

Donn Eric Rosen was an ichthyologist at the American Museum of Natural History for most of his career, which ended abruptly with his death at age 57 (see Nelson et al., 1987). Donn was a native New Yorker and the younger brother of Charles Rosen, a renowned classical pianist, musicologist, and literary critic.

Donn Rosen's influential studies of the systematics and biogeography of livebearing fishes of the genera *Xiphophorus* and *Heterandria* (family Poeciliidae) quickly became benchmarks of the application of cladistic methods in biogeography. AMNH colleague, ichthyologist, and biogeographer Gareth Nelson; the late British paleontologist Colin Patterson; and the late British ichthyologist P. Humphry Greenwood were among his closest collaborators.

Rosen was a gifted teacher and, through his appointment as an adjunct professor at the City University of New York, served as major professor to a series of doctoral students, notably for biogeography including E. O. Wiley, Richard Vari, Lance Grande, and Lynne Parenti. Despite their philosophical differences, especially over the significance of the biological species concept, Rosen and Ernst Mayr, a curator at the AMNH before becoming a professor at Harvard University, maintained a cordial relationship. Rosen married Carmela Berritto, a former classmate at New York University and Mayr's research assistant at the AMNH, who co-authored a study of geographic variation in Bahamian snails (Mayr and Rosen, 1956; see Chapter 2).



Norman Platnick

BIOGEOGRAFIA CLADÍSTICA

Nelson 1974, D. Rosen 1976, Nelson & Platnick 1981

Correspondência entre as relações filogenéticas de grupos de organismos e as relações entre as áreas geográficas é biogeograficamente informativa

Busca um padrão nas relações entre as áreas de endemismo, que se encontre repetidamente na filogenia de táxons diversos e que possa relacionar-se com eventos da história da Terra.

BIOGEOGRAFIA CLADÍSTICA

fundamentos

Construção de **cladogramas de áreas** a partir de cladogramas de táxons.

Construção de um ou mais **cladogramas gerais de áreas** a partir das congruências daqueles anteriores.

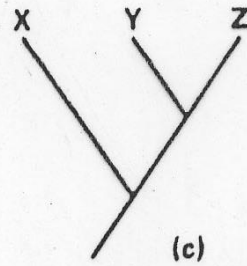
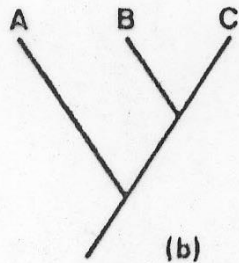
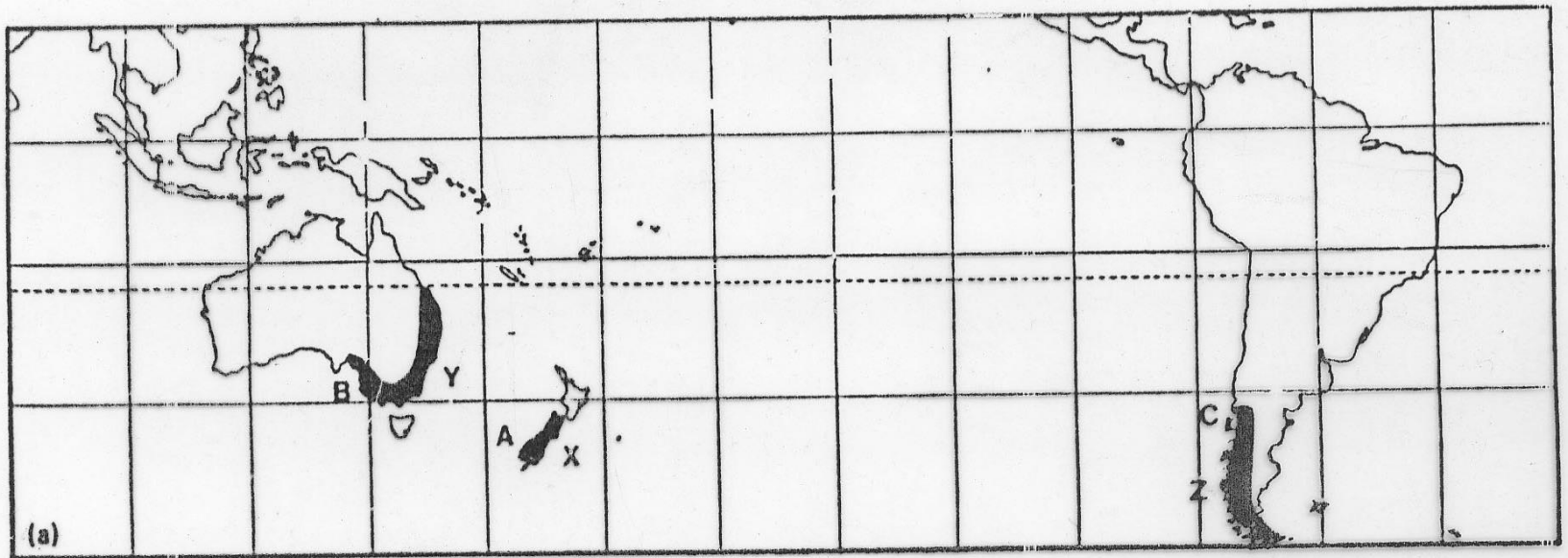


Fig. 2.8. (a) Hypothetical distribution of two groups—fishes (A, B, C) and flowering trees (X, Y, Z). (b, c) Cladograms for each group.

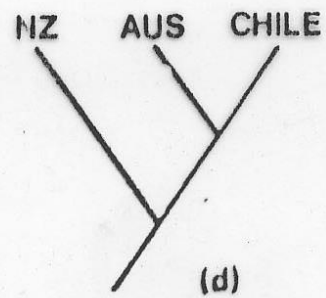
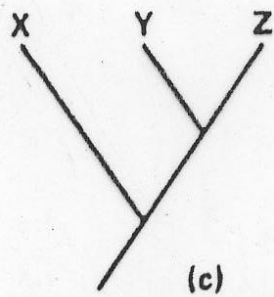
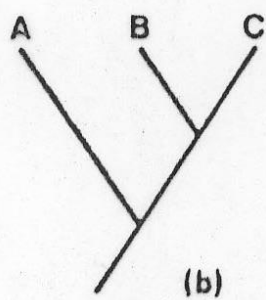
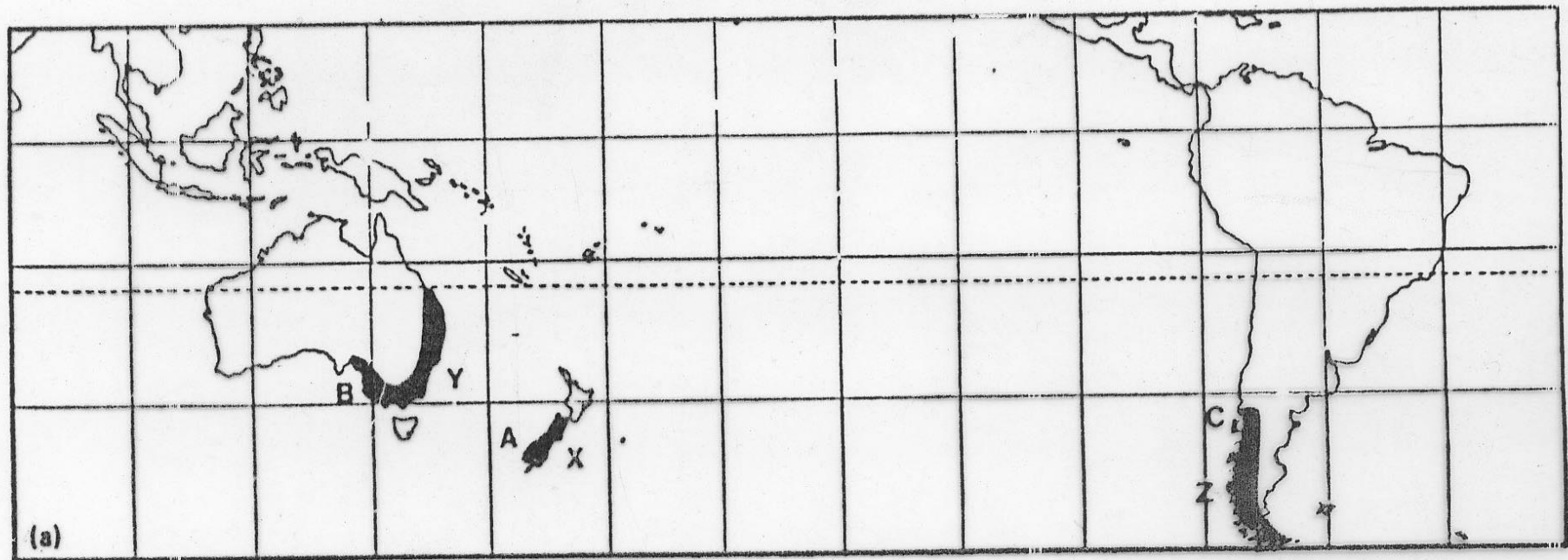
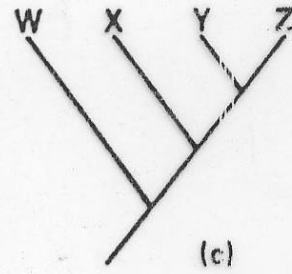
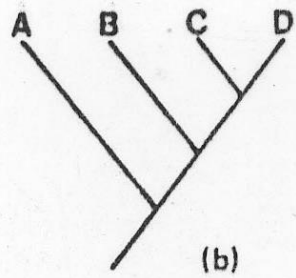
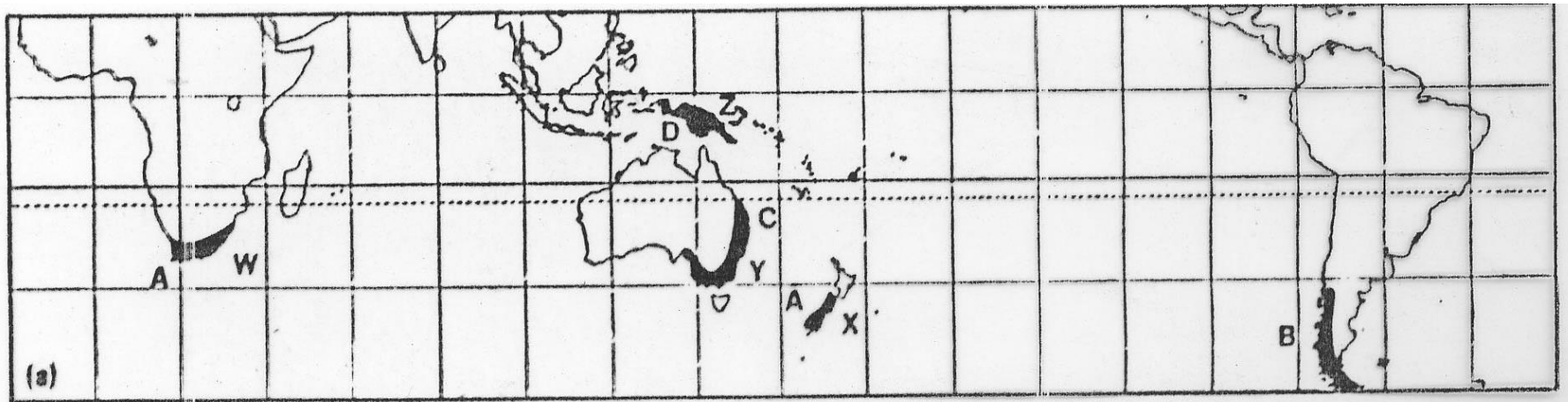


Fig. 2.8. (a) Hypothetical distribution of two groups—fishes (A, B, C) and flowering trees (X, Y, Z). (b, c) Cladograms for each group. (d) Area cladogram common to both groups.



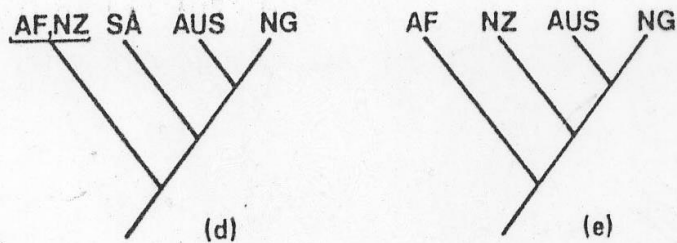
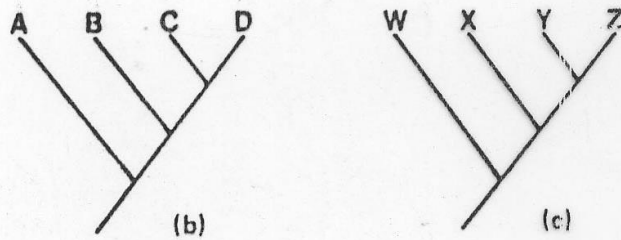
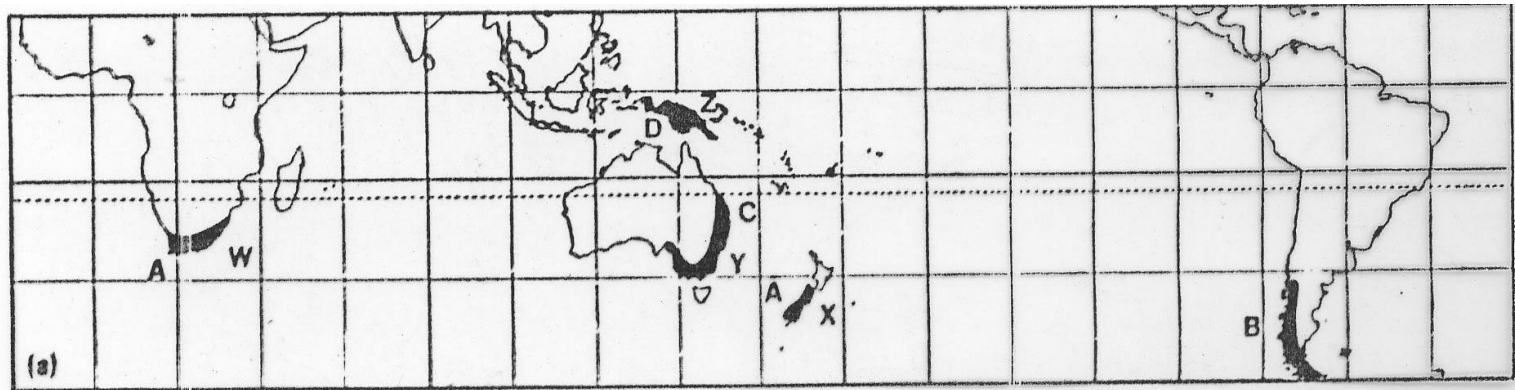


Fig. 2.9. (a) Hypothetical distribution of two groups—fishes (A-D) and flowering trees (W-Z) in the southern hemisphere. (b, c) Cladograms for each group. (d, e) Area cladograms for each group.

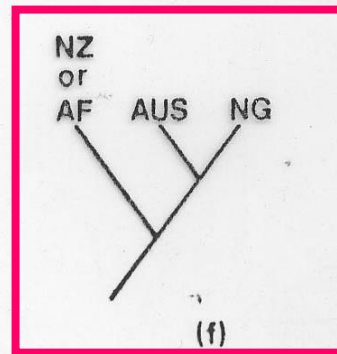
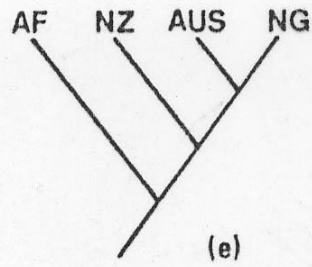
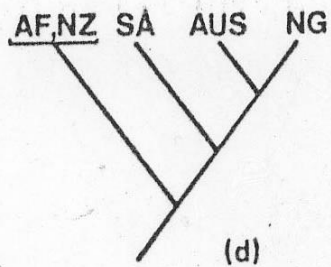
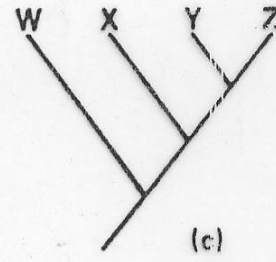
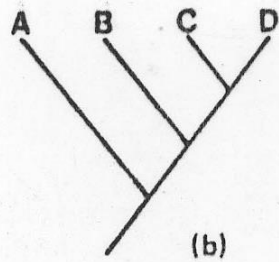
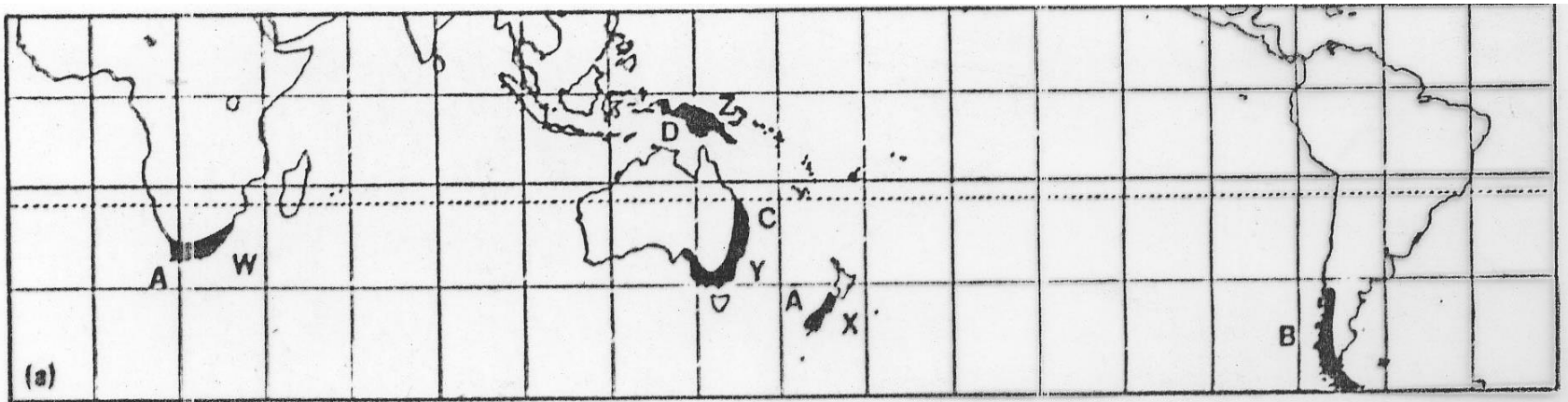
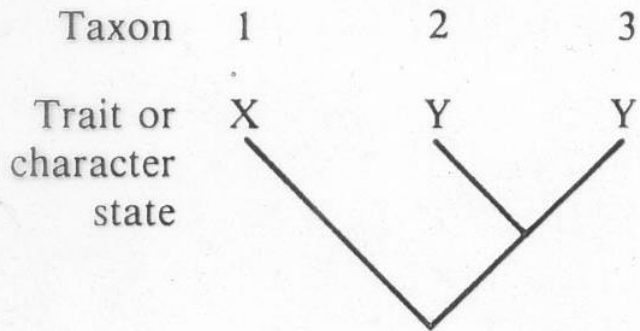
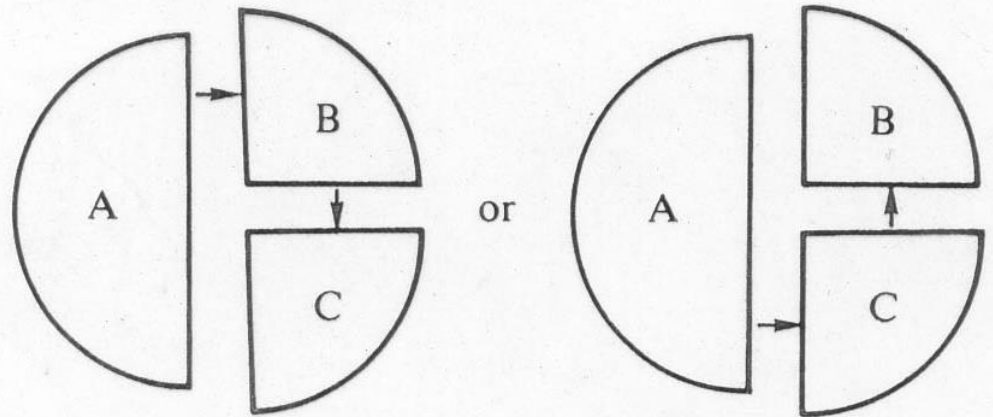


Fig. 2.9. (a) Hypothetical distribution of two groups—fishes (A-D) and flowering trees (W-Z) in the southern hemisphere. (b, c) Cladograms for each group. (d, e) Area cladograms for each group. (f) reduced area cladograms.

Cladogram



Dispersal hypothesis



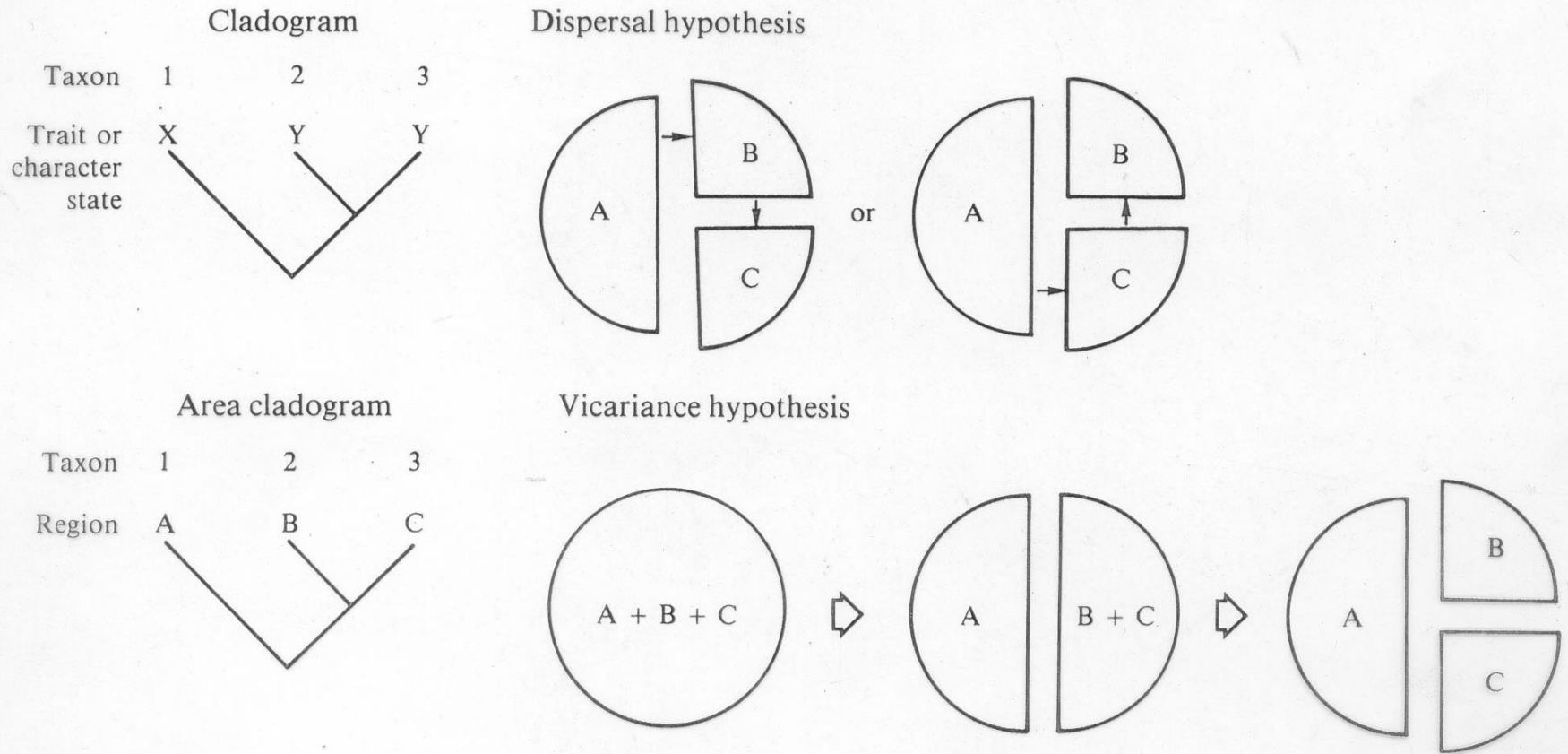
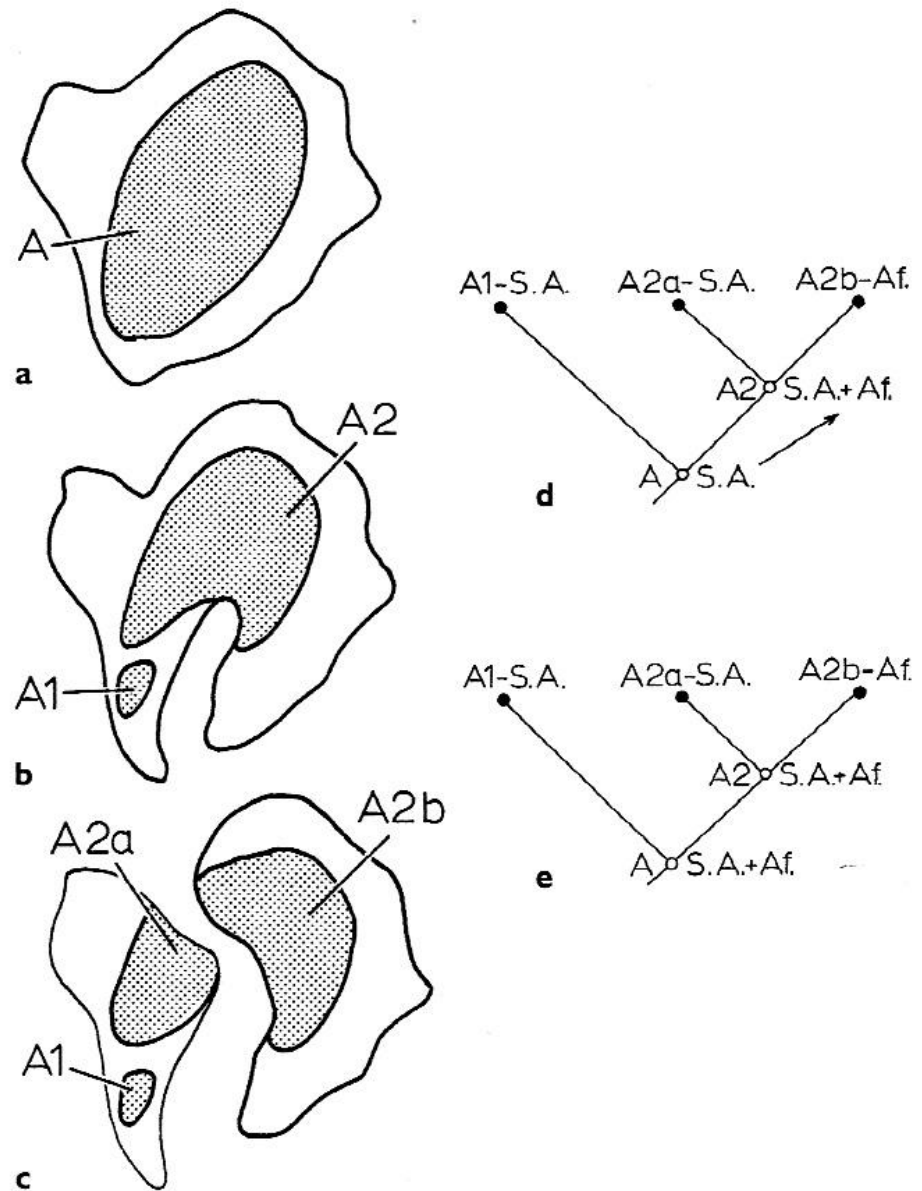


Figure 9.9

Hypothetical cladogram showing presumed phylogenetic relationships among three taxa, and corresponding dispersal and vicariance hypotheses to account for their distribution. Note that even without any extinctions and multiple colonizations there are two dispersal hypotheses that account equally well for the known data, but only a single area cladogram and vicariance hypothesis.

Figure 3.7 Vicariance of an ancestral species widespread in South America and Africa: (a) ancestral species A; (b) vicariance of species A into descendant species A1 and A2; (c) subsequent splitting of A2 into descendant species A2a and A2b; (d) dispersal interpretation; (e) vicariance interpretation (modified from Nelson 1974:556; reproduced with permission of *Systematic Biology*).

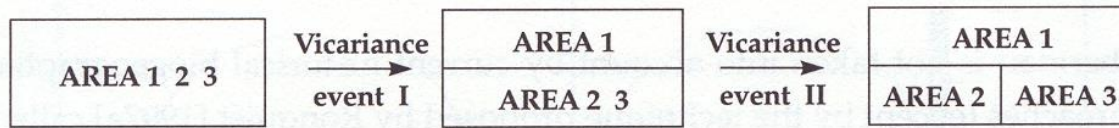
**Nelson 1974,
reproduzido em
Morrone 2009**



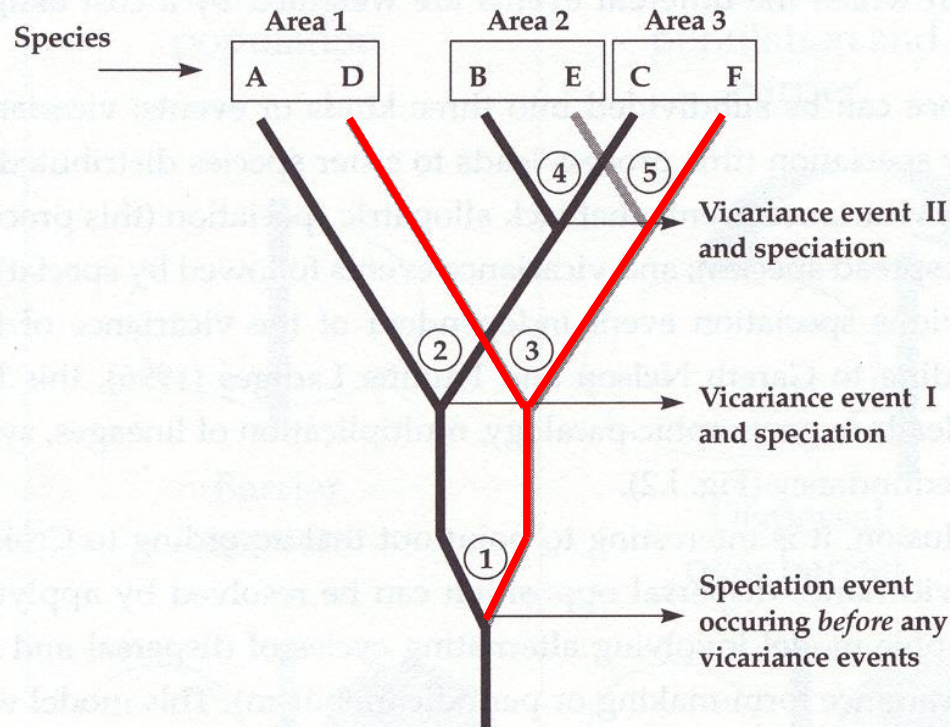
VICARIÂNCIA

1. Eventos de vicariância + especiação
= espécies-irmãs em áreas-irmãs
2. Eventos de vicariância + especiação *a posteriori*
de uma especiação prévia independente da vicariância
= **paralogia geográfica** (ou simpatria, ou redundância)
3. Eventos de vicariância sem especiação
= espécie de ampla distribuição

GEOGRAPHIC PARALOGY



Paralogia geográfica



Crisci *et al.* 2003

Geographic paralogy as a result of a speciation event (1) independent of area vicariance. Two subsequent speciation events (2, 3) are related with vicariant event I, and two subsequent speciation events (4, 5) are related with vicariant event II.

BIOGEOGRAFIA CLADÍSTICA - métodos

Problemas frequentes no processo de construção de **cladogramas de áreas** a partir de cladogramas de táxons:

- áreas ausentes
- distribuições redundantes (paralogia)
- táxons amplilocados (distribuição ampla) (paralogia)

Nessas 3 situações deve-se assumir 1 a 3 suposições para a obtenção de cladogramas resolvidos

3 suposições possíveis
para obtenção de
cladogramas resolvidos,
no caso de táxon
amplamente distribuído
nas áreas 1 e 2

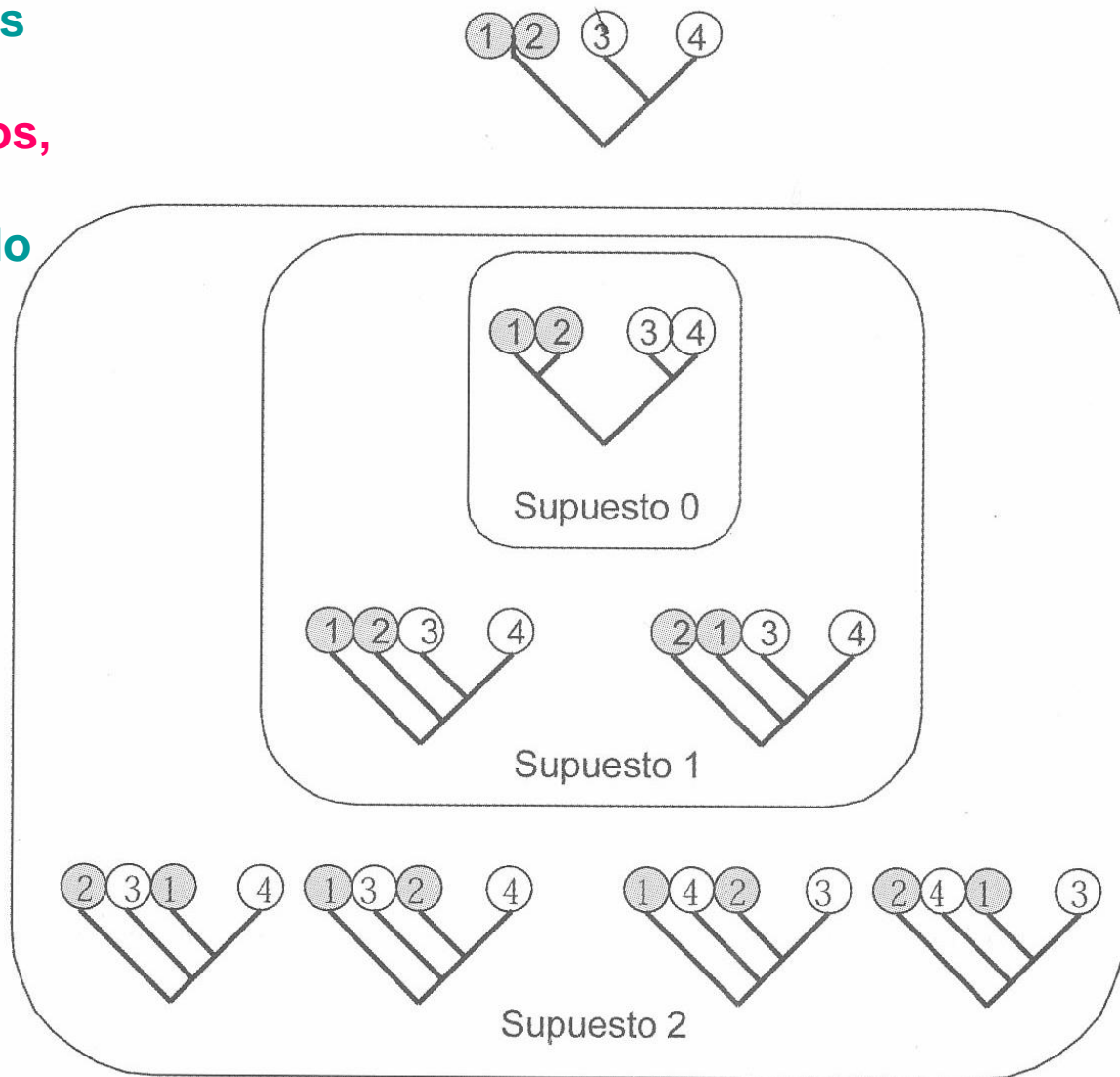


Fig. IX-2. Cladograma de áreas con un taxón ampliamente distribuido en las áreas 1 y 2, y obtención de los cladogramas de áreas resueltos según los supuestos 0, 1 y 2 (modificado de Morrone & Crisci, 1995).

BIOGEOGRAFIA CLADÍSTICA - métodos

Construção de um ou mais **cladogramas gerais de áreas** a partir das congruências daqueles anteriores:

Análise de componentes – COMPONENT 1.5 (Page 1989)

Parcimônia quantitativa ou BPA (parcimônia de Brooks, 1985, 1990; Wiley 1987)
– algoritmo de Wagner (Kluge & Farris 1969).

Enunciados de 3 áreas ou TAS (Nelson & Ladiges 1991)

Análise de Componentes

Nelson & Platnick 1981, modificado por Page 1989 (COMPONENT 1.5)

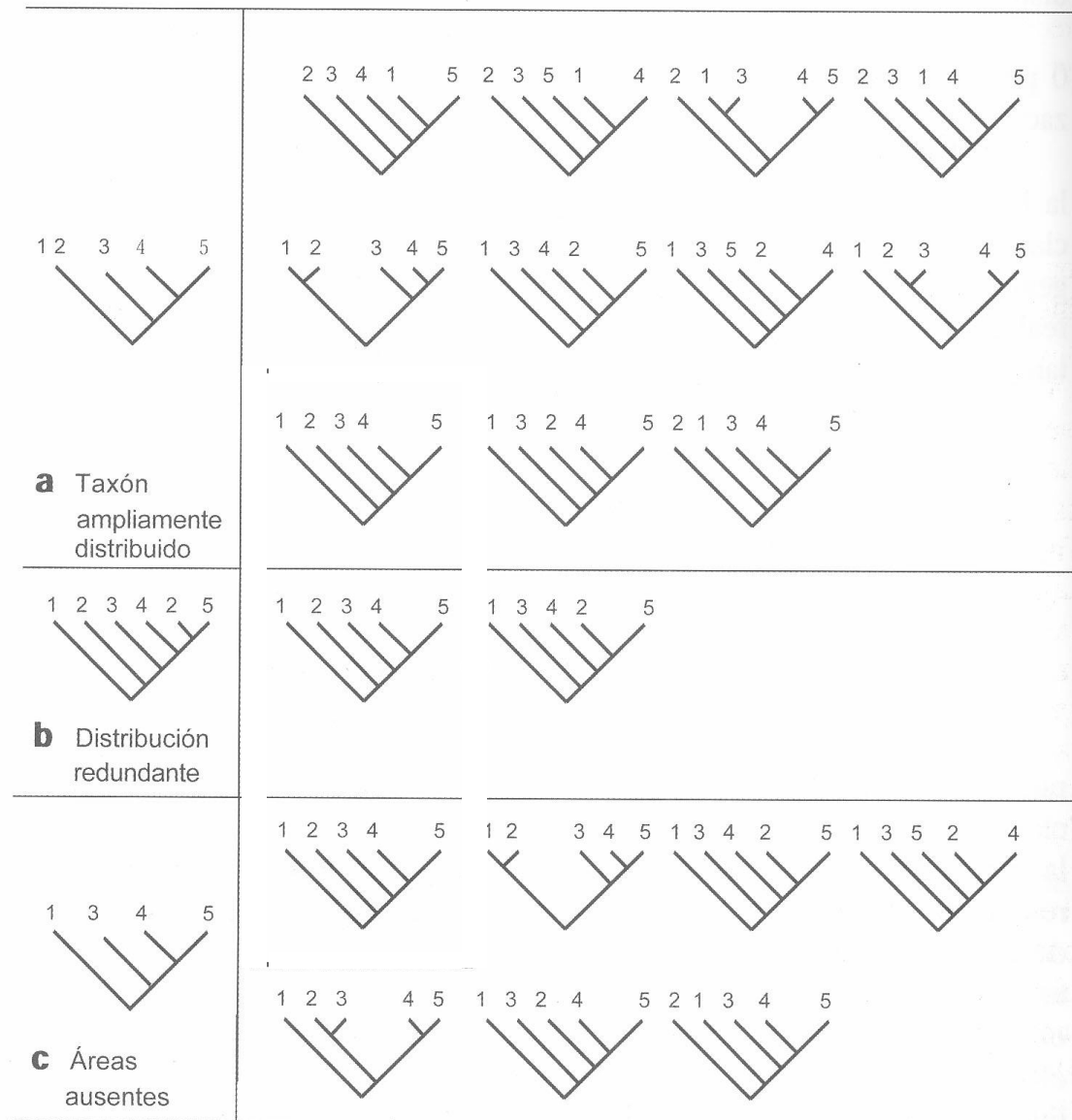


Fig. IX-3. Aplicación del método análisis de los componentes aplicando el supuesto 2. a, Cladograma de áreas con un taxón ampliamente distribuido; b, cladograma de áreas con una distribución redundante; c, cladograma de áreas con un área ausente. La intersección de los tres conjuntos de cladogramas de áreas resueltos (indicados con un recuadro) corresponde al cladograma general de áreas (modificado de Morrone & Crisci, 1995).

Análise de Componentes

Nelson & Platnick 1981, modificado por Page 1989 (COMPONENT 1.5)

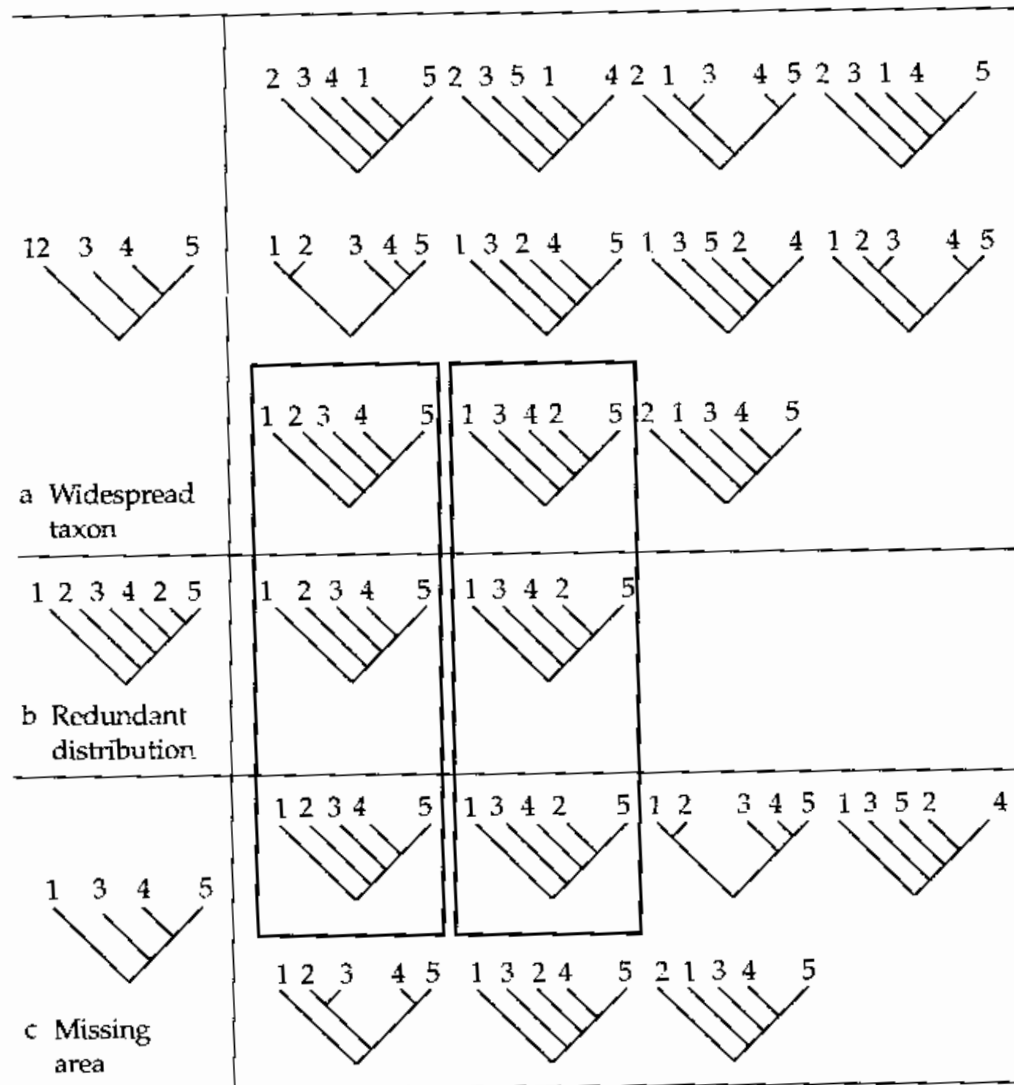


FIGURE 6.3. Application of component analysis using assumption 2. (a) Area cladogram including a widespread taxon; (b) area cladogram including a redundant distribution; (c) area cladogram including a missing area. Intersection of the three sets of resolved area cladograms (marked with squares) represents the general area cladograms. Areas: 1-5.

Matrizes de áreas x componentes do cladograma

BPA

Análise de Parcimônia de Brooks

(Wiley 1987,
baseado em idéias de
Brooks 1985)

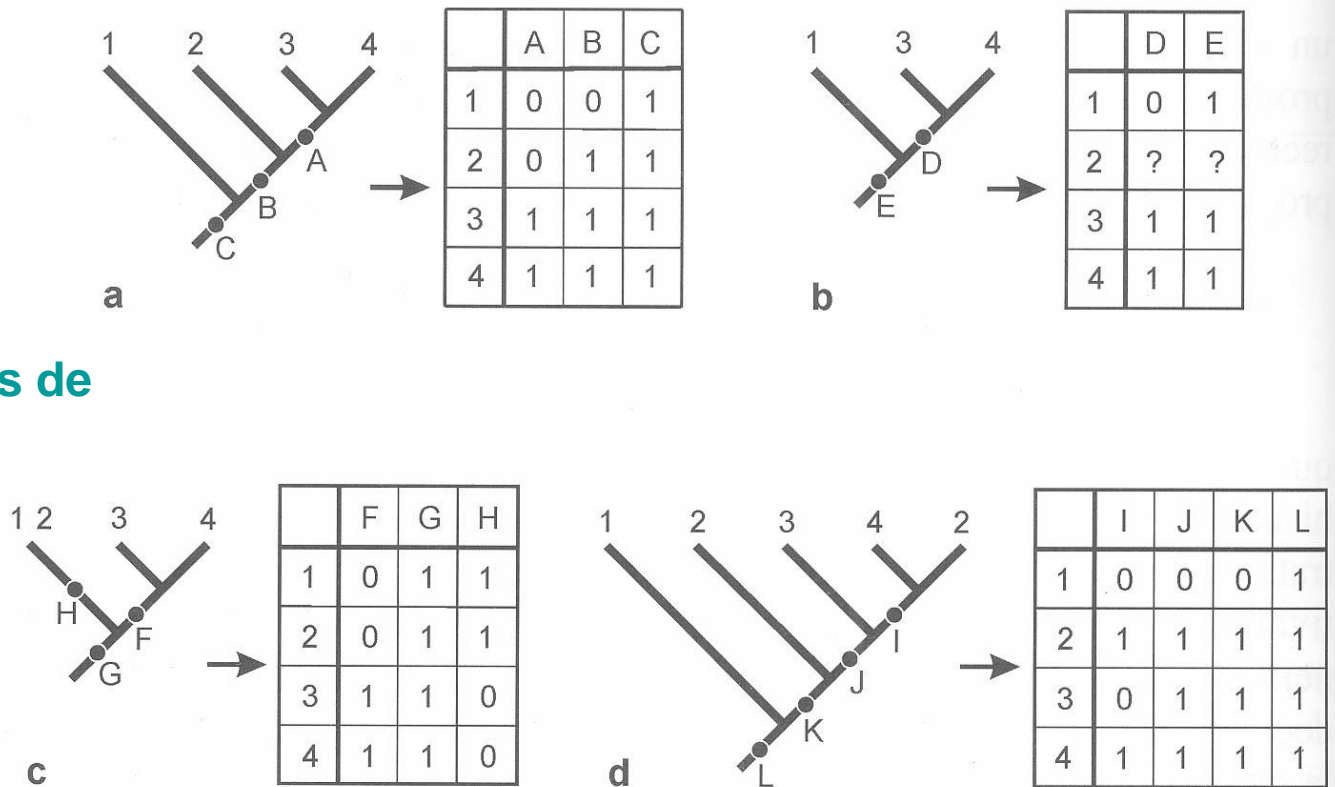
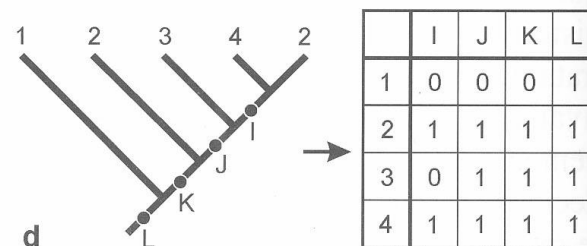
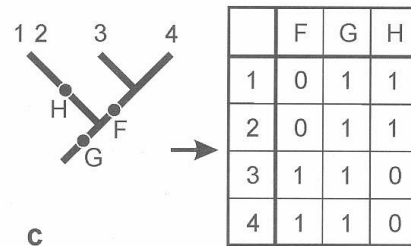
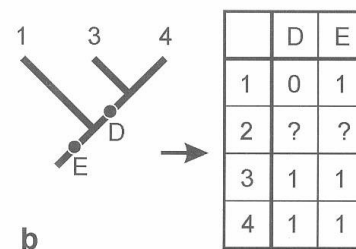
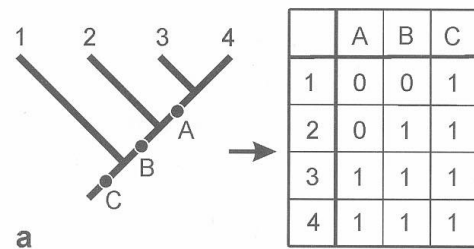


Fig. IX-4. Simplicidade quantitativa. a, Cladograma de áreas com los dados completos y sin ambigüedad; b, cladograma de áreas con un área ausente; c, cladograma de áreas con un taxón ampliamente distribuido; d, cladograma de áreas con una distribución redundante; e,



	A	B	C	D	E	F	G	H	I	J	K	L
1	0	0	1	0	1	0	1	1	0	0	0	1
2	0	1	1	?	?	0	1	1	1	1	1	1
3	1	1	1	1	1	1	1	0	0	1	1	1
4	1	1	1	1	1	1	1	0	1	1	1	1



BPA

Análise de Parcimônia de Brooks

(Wiley 1987, baseado em idéias de Brooks 1985)

Combinar todas as matrizes em uma **matriz geral**
 (adicionar coluna ancestral codificada com 0 em todas as entradas)
 (aplicar **algoritmo de parcimônia** – Hennig 86 (Farris 1988),
 ou PAUP (Swofford 2000, 2008) ou PHYLIP (Felsenstein 1993)
 ou NONA (Goloboff 1996, 2004, 2009)

BPA

Análise de Parcimônia de Brooks

(Wiley 1987, baseado em idéias de Brooks 1985)

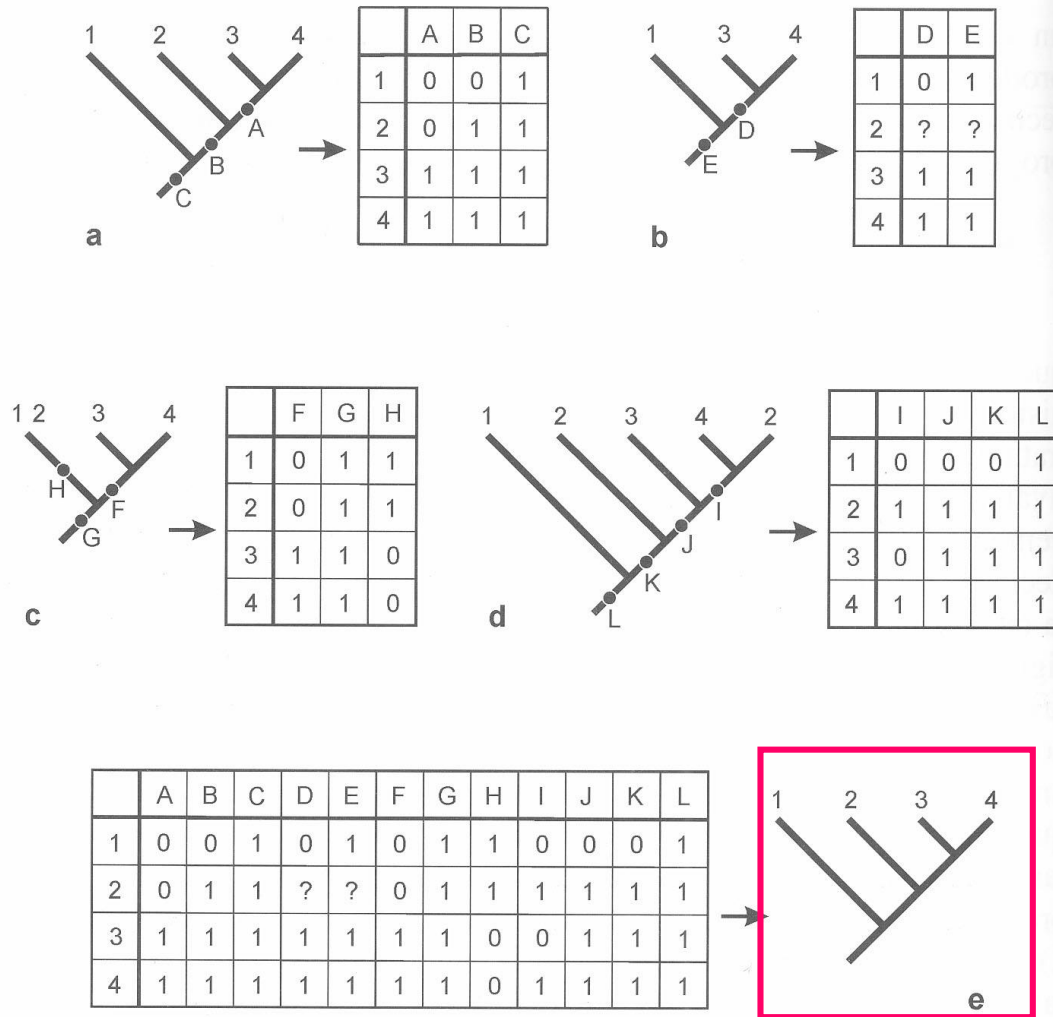


Fig. IX-4. Simplicidad cuantitativa. a, Cladograma de áreas con los datos completos y sin ambigüedad; b, cladograma de áreas con un área ausente; c, cladograma de áreas con un taxón ampliamente distribuido; d, cladograma de áreas con una distribución redundante; e, matriz de datos (áreas por componentes) y cladograma general de áreas resultante obtenido al aplicar un algoritmo de simplicidad. 1-4 áreas; A-L componentes (modificado de Morrone & Crisci, 1995).

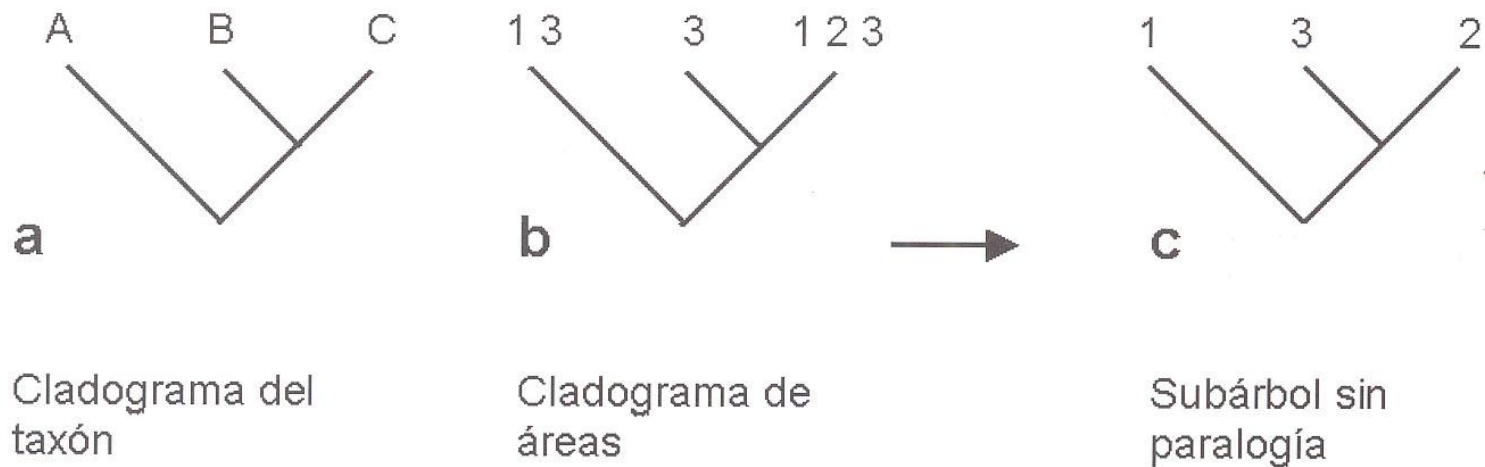
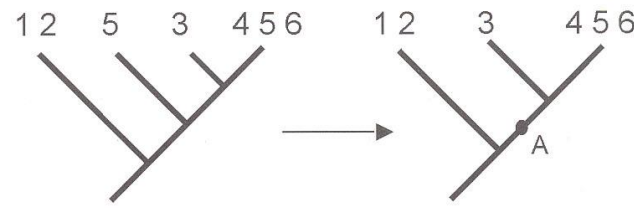


Fig. IX-6. Subárboles sin paralogía. a, Cladograma del taxón formado por las especies A, B y C; b, conversión en cladograma de áreas, 1, 2 y 3 representan las áreas donde están distribuidos los taxones A, B y C, se observa paralogía ya que el área 3 está habitada por los tres taxones y el área 1 está habitada por los taxones A y C; c, subárbol sin paralogía.

Subárvores sem paralogia

Nelson & Ladiges 1996

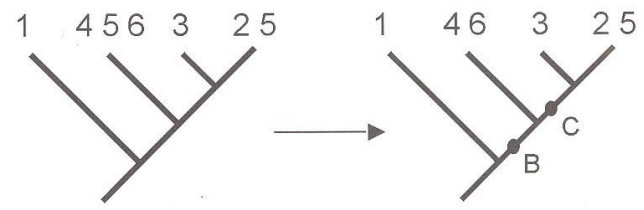
algoritmo TASS



a Cladograma de áreas

Subárbol sin paralogía

	A
OG	0
1	0
2	0
3	1
4	1
5	1
6	1



b Cladograma de áreas

Subárbol sin paralogía

	B	C
OG	0	0
1	0	0
2	1	1
3	1	1
4	1	0
5	1	1
6	1	0

c

	A	B	C
OG	0	0	0
1	0	0	0
2	0	1	1
3	1	1	1
4	1	1	0
5	1	1	1
6	1	1	0

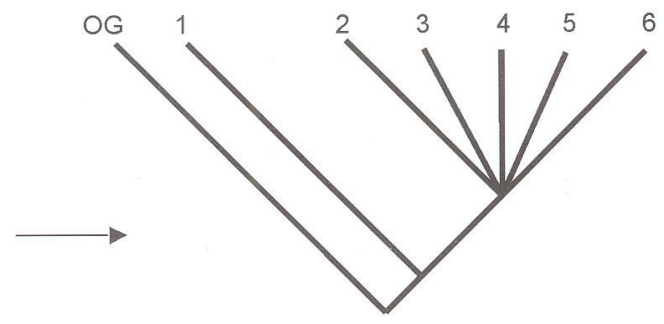


Fig. IX-7. Subárboles sin paralogía. a y b, Dos cladogramas de áreas correspondientes a dos taxones distintos mostrando sus respectivos subárboles sin paralogía y las matrices de áreas por componentes correspondientes a cada uno de ellos, a partir de la aplicación del programa TASS; c, matriz de áreas por componentes resultante de la unión de las matrices de a y b y cladograma general de áreas obtenido aplicando un algoritmo de simplicidad. 1-6= áreas; A-C= componentes; OG= área externa hipotética.

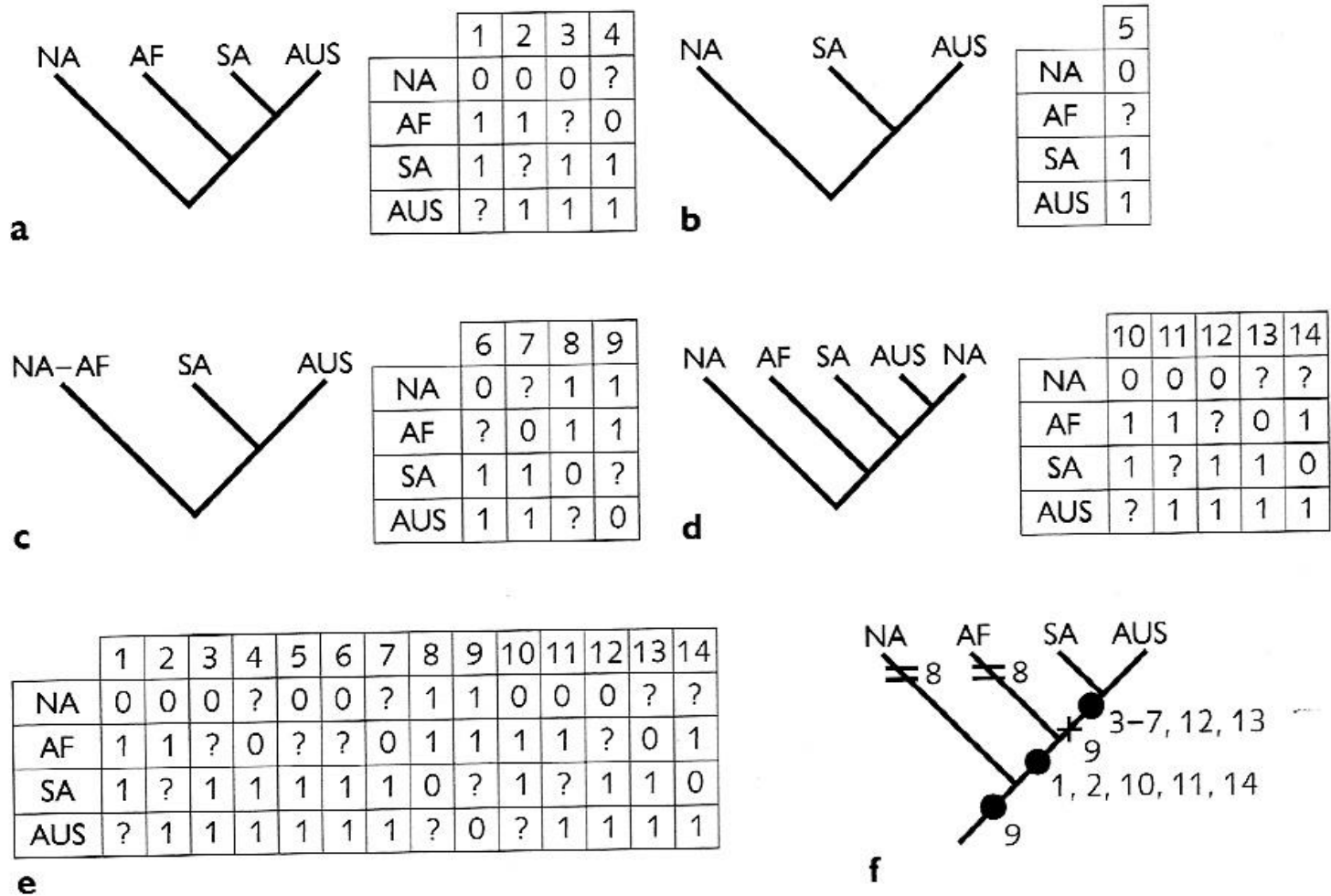


Figure 5.13 Three area statement analysis. (a–d) Taxon–area cladograms and matrices derived from them: (a) trivial case; (b) taxon with a missing area; (c) widespread taxon; (d) taxon with a redundant distribution; (e) data matrix with all the information; (f) general area cladogram obtained. AF, Africa; AUS, Australia; NA, North America; SA, South America.

BIOGEOGRAFIA CLADÍSTICA

Exemplos:

Biogeogr. cladística dos territórios austrais:
Humphries 1981 (usando *Nothofagus* e mais 20 grupos animais e vegetais, incluindo fósseis);
Linder & Crisp 1995 (usando novos táxons e dados, incluindo moleculares).

Crisci *et al.* 1991 – biogeogr. cladística da América do Sul meridional, usando 17 táxons de fungos (1), vegetais (8) e animais (8)

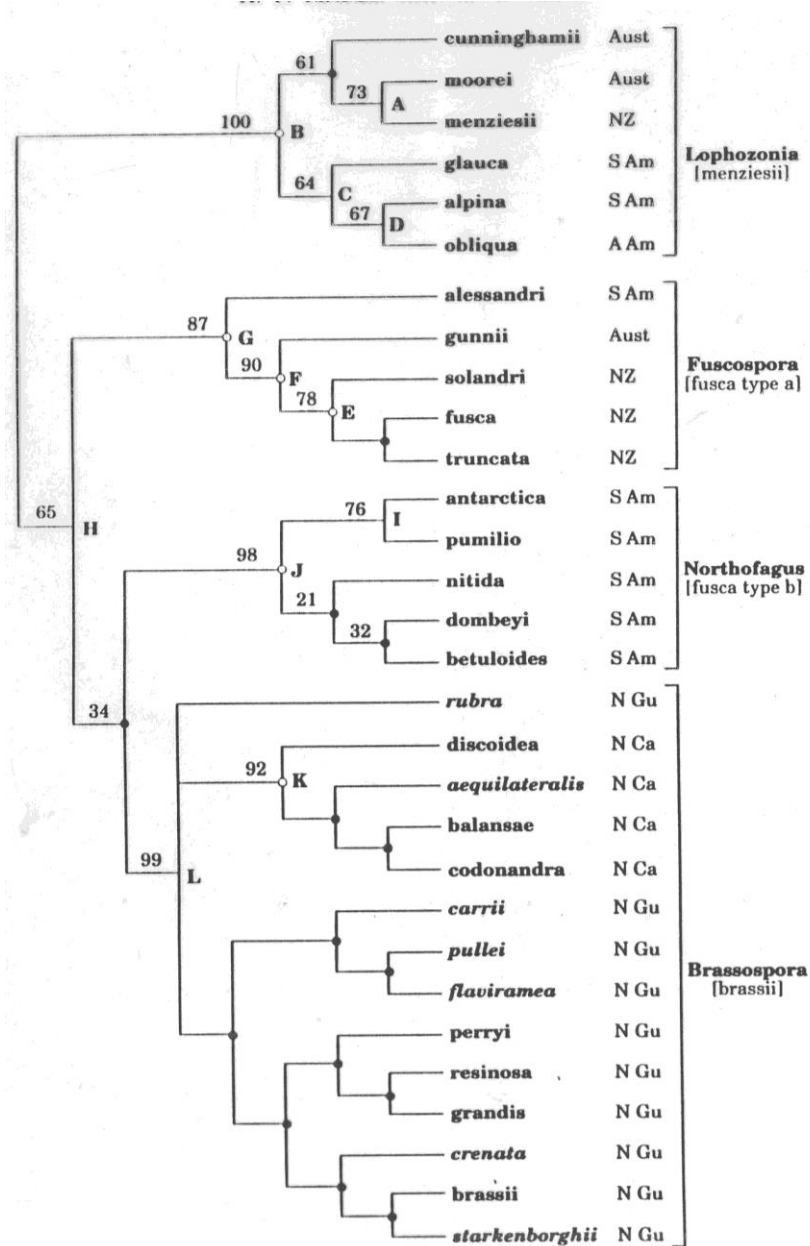


Fig. 3. Hypothesized phylogenetic tree for *Nothofagus*, using morphological and molecular (*rbd*, sequence) data. Taxa for which molecular data are not available are inserted on the evidence of the morphological data. Open circles indicate nodes found in a consensus analysis of separate morphological and molecular trees; closed circles indicate nodes not common to all minimal length trees from the total evidence analysis. Pollen types are shown in square brackets below the subgeneric classification. Bootstrap values are indicated below the nodes.

Nothofagus
Linder & Crisp 1995

Fig. 5. Phylogeny for Iridaceae, with the areas plotted on the trees.

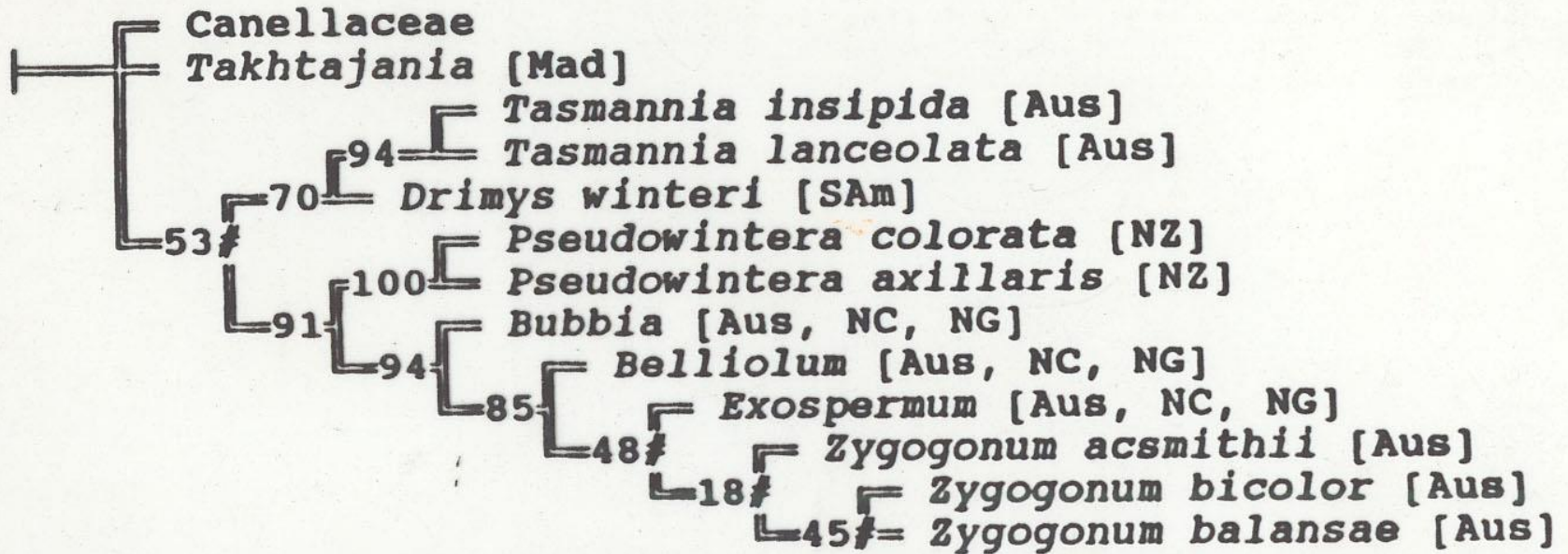


Fig. 6. One of the eight minimal length trees located for combined molecular and morphological data sets of Winteraceae. The length is 105 steps, the retention index 90. Nodes which collapse in the strict consensus tree are indicated by hashes; bootstrap percentiles from 500 resampled replicate data sets are indicated on the branches. The distribution areas for each species are plotted onto the cladogram.

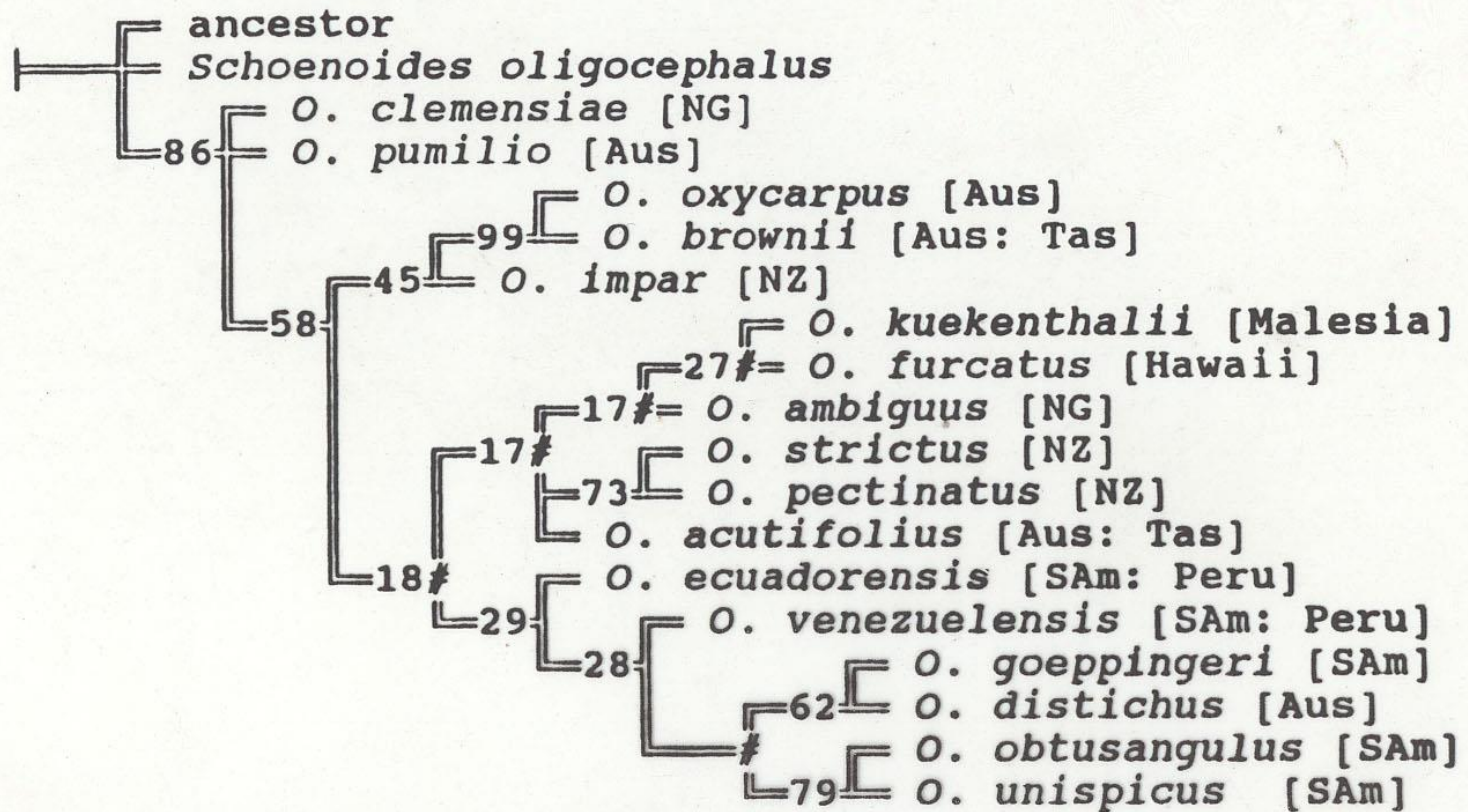
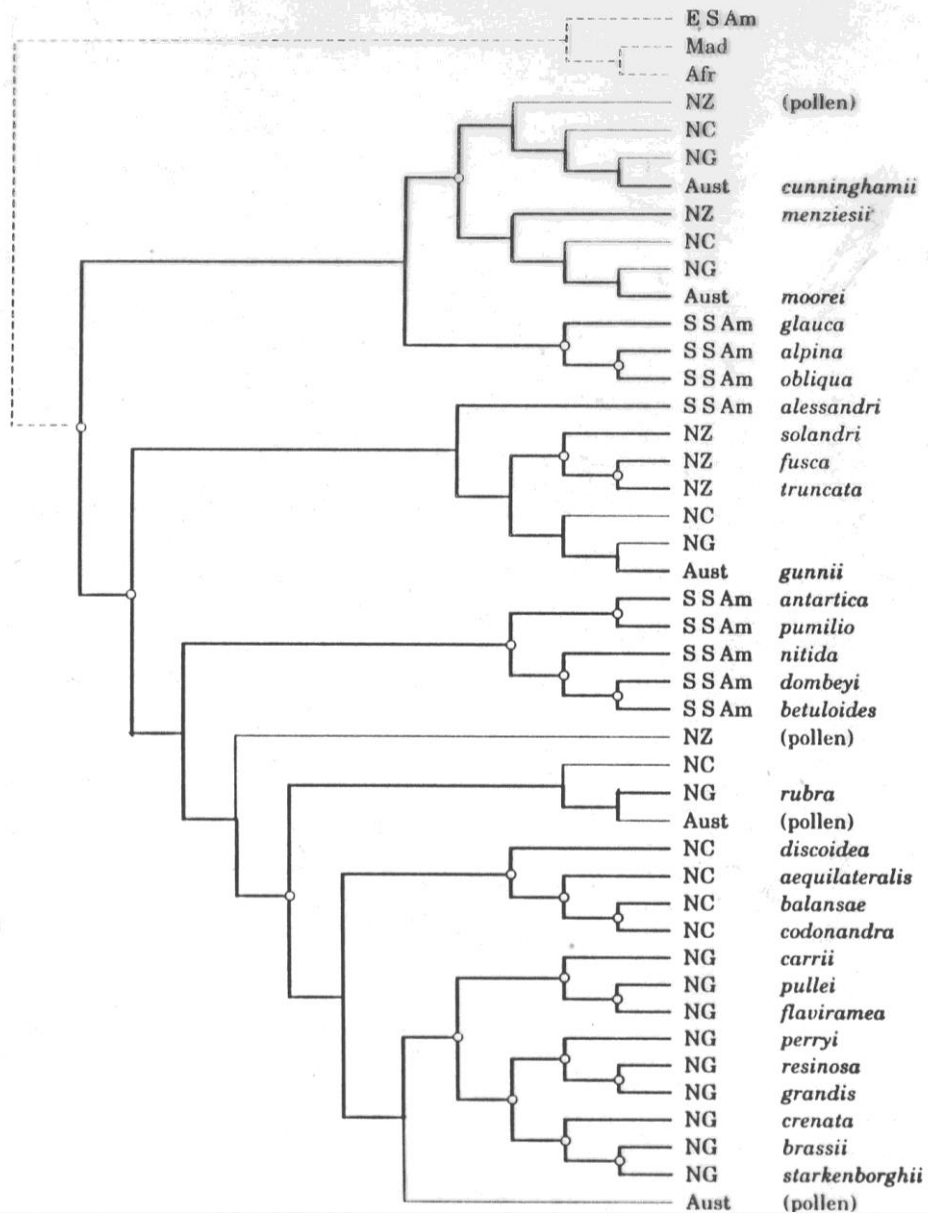


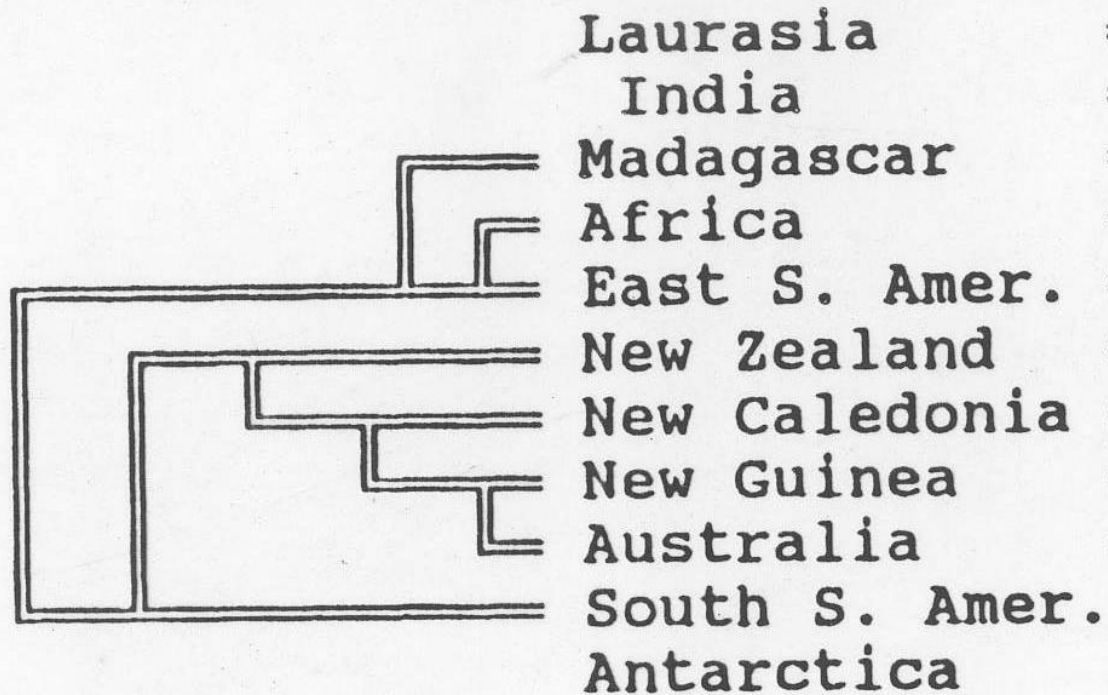
Fig. 8. Tree for *Oreobolus* (Cyperaceae) located by successive weighting from the set of 10 most parsimonious trees. Nodes which collapse in the strict consensus tree are indicated with hashes; bootstrap percentiles from 500 resampled replicate data sets are indicated on the branches. The distribution areas for each species are plotted onto the cladogram.



Nothofagus Linder & Crisp 1995

Fig. 10. Reconciliation between the general area-cladogram and the cladogram for *Nothofagus*. Circles indicate duplication of components (equivalent to sympatric speciation events). Thick lines indicate those components of the general area-cladogram that are represented by extant taxa; thin lines indicate missing components (no extant taxon); dashed lines indicate components for which *Nothofagus* is uninformative.

a. Area relationships
(from plants)

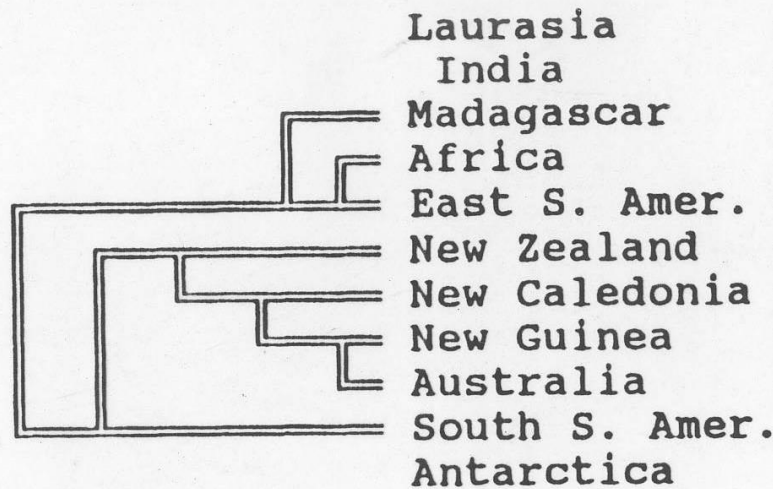


General area-cladogram, constructed using Page's (1994) modification of component analysis,

Nothofagus

Linder & Crisp 1995

a. Area relationships
(from plants)



b. Conventional geological
History

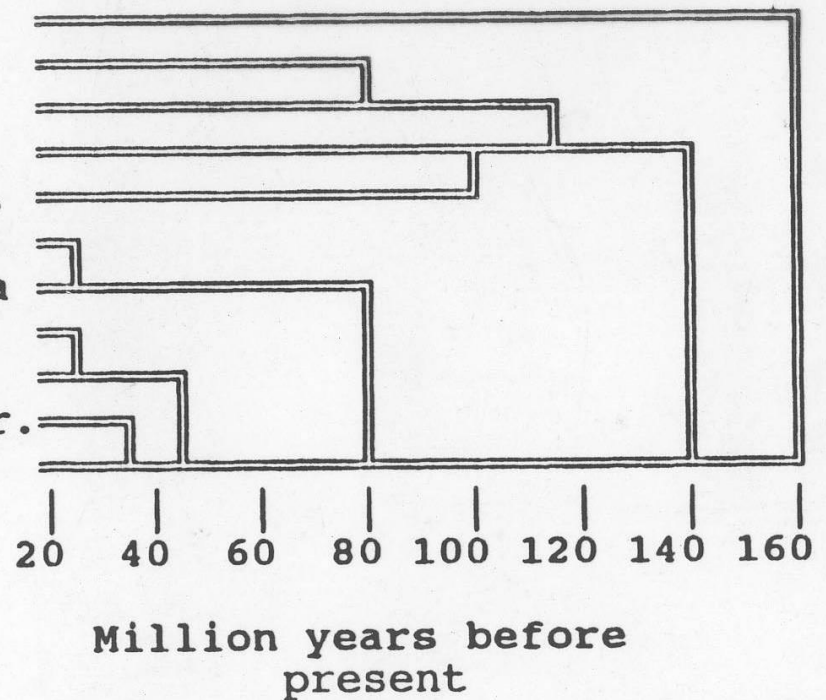


Fig. 9. General area-cladogram, constructed using Page's (1994) modification of component analysis, and matched against a reconstruction of geological vicariance events, based on Scotese et al. (1988). An approximate time-scale is indicated below the diagram.

Monocalyptus

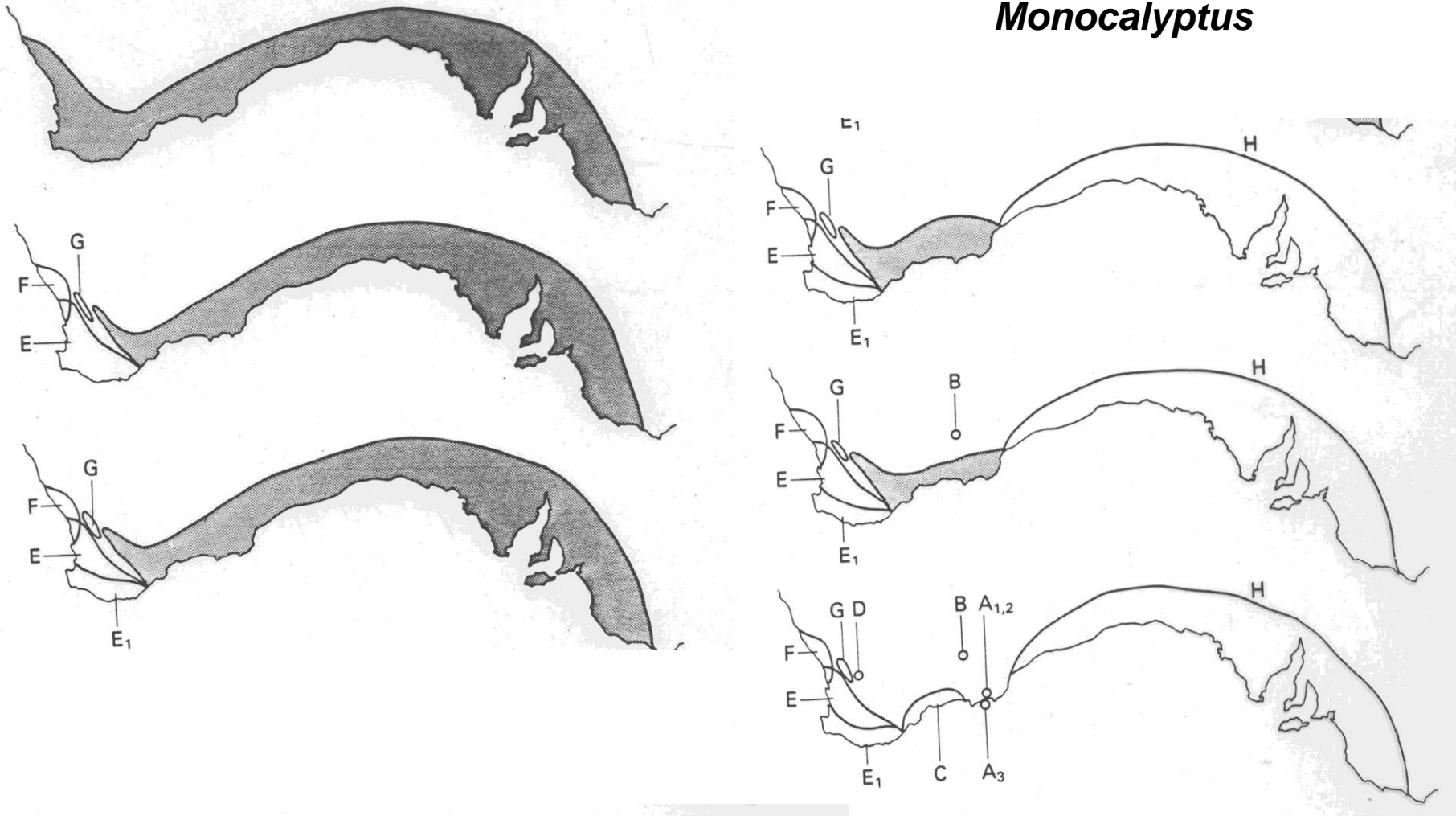


Fig. 9.4 The hypothetical sequence of changes in distribution pattern of the eucalypt tree *Monocalyptus* in southern Australia, after Humphries *et al.* [7]. The area marked in black is the continuous, hypothetical range of one particular species at each period of time from the earliest (top) to today (bottom). This becomes progressively, vicariantly subdivided into the ranges of the living species, A–H.

Roscoea
Zingiberaceae

Ngamriabsakul et al. 2000

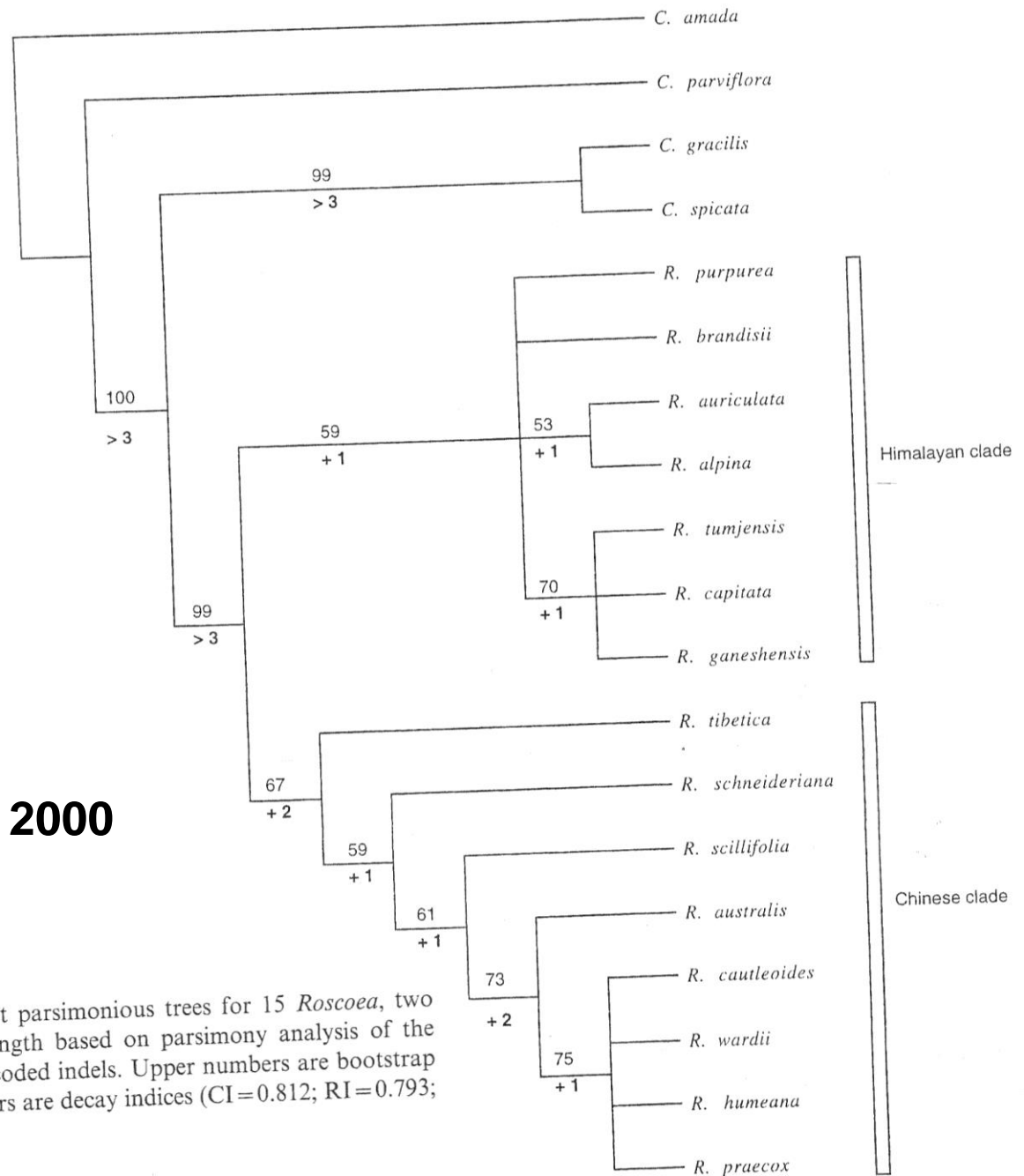


FIG. 3. Strict consensus tree based on five most parsimonious trees for 15 *Roscoea*, two *Cautleya* and two *Curcuma* taxa of 213 steps length based on parsimony analysis of the combined ITS1 and ITS2 sequence data plus the coded indels. Upper numbers are bootstrap values of 1000 replicates. Lower (boldface) numbers are decay indices (CI=0.812; RI=0.793; RC=0.644).

Roscoea
Zingiberaceae

Ngamriabsakul et al. 2000

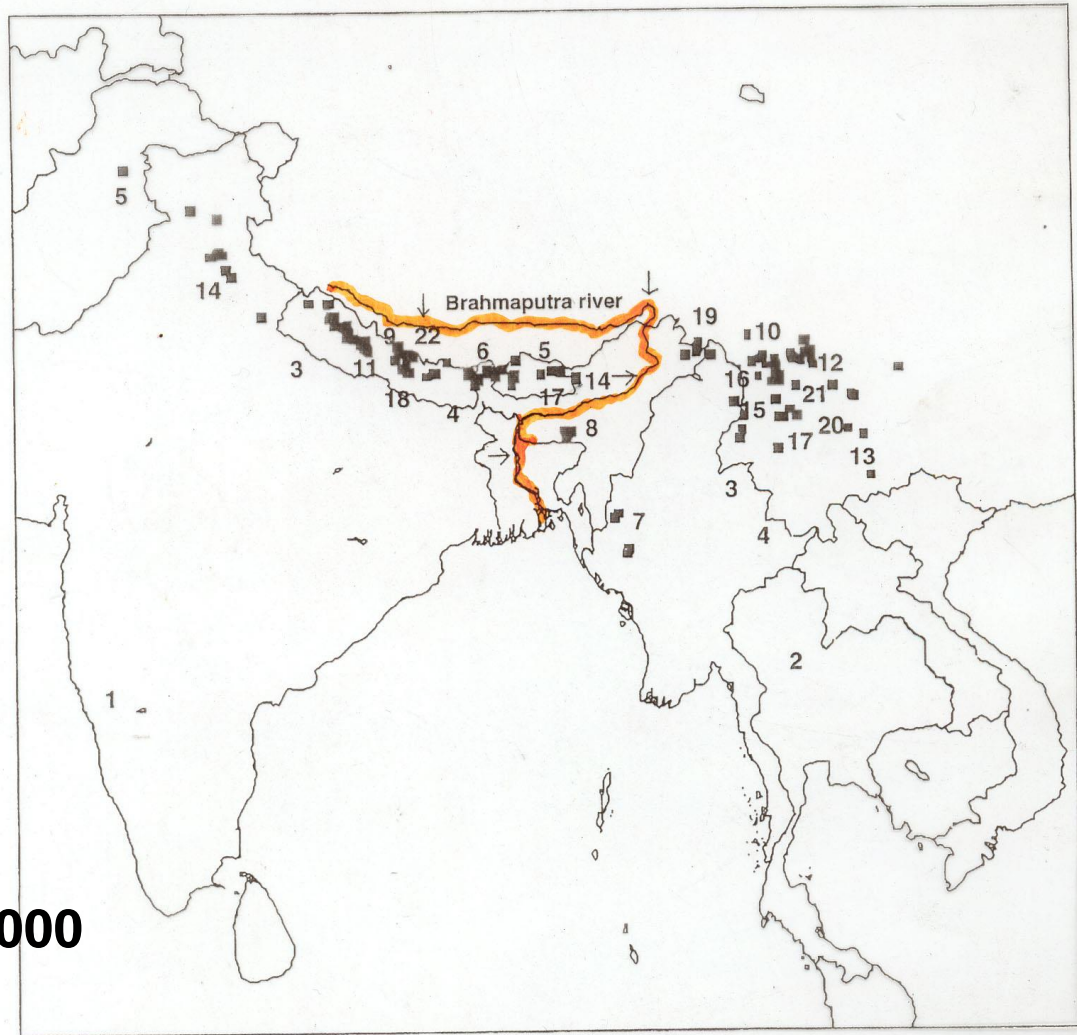
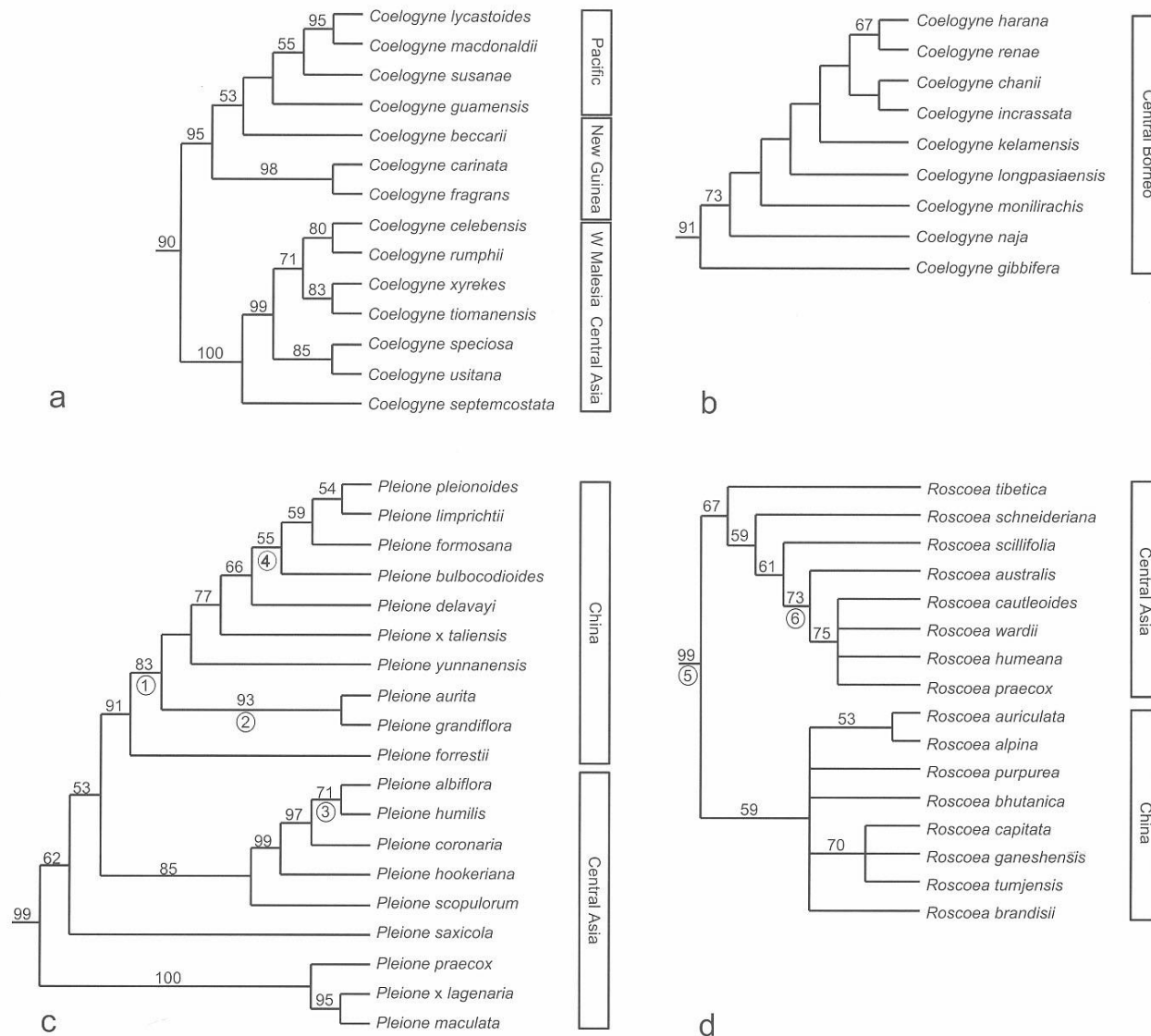


FIG. 1. Simplified geographical distribution of *Roscoea* species described to date (number 5 to 19 referring to the species listed in Table 1; number 20 = *Roscoea debilis*, number 21 = *Roscoea forrestii*, number 22 = *Roscoea nepalensis*). The position of the number is an indication of the species (note. two species, i.e. *Roscoea alpina* and *Roscoea purpurea* are widespread along the Himalaya). *Cautleya gracilis* (number 3) and *Cautleya spicata* (number 4) occur both in the Himalaya and China. *Curcuma* species numbers (1 and 2) only indicate the origin of samples. Arrows show the course of the Brahmaputra river.



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Fig. 1. Total evidence phylogenies of (a) *Coelogyne* section *Speciosae* (from Gravendeel & de Vogel, 1999; Gravendeel, 2000); (b) *Coelogyne* section *Moniliformes* (from Gravendeel & de Vogel, 2002); (c) *Pleione* (from Gravendeel & al., 2004); (d) *Roscoea* (from Ngamriabsakul & al., 2000); strictly vicariant nodes (see text) are indicated by numbers in circles, bootstrap support values are indicated above corresponding nodes.

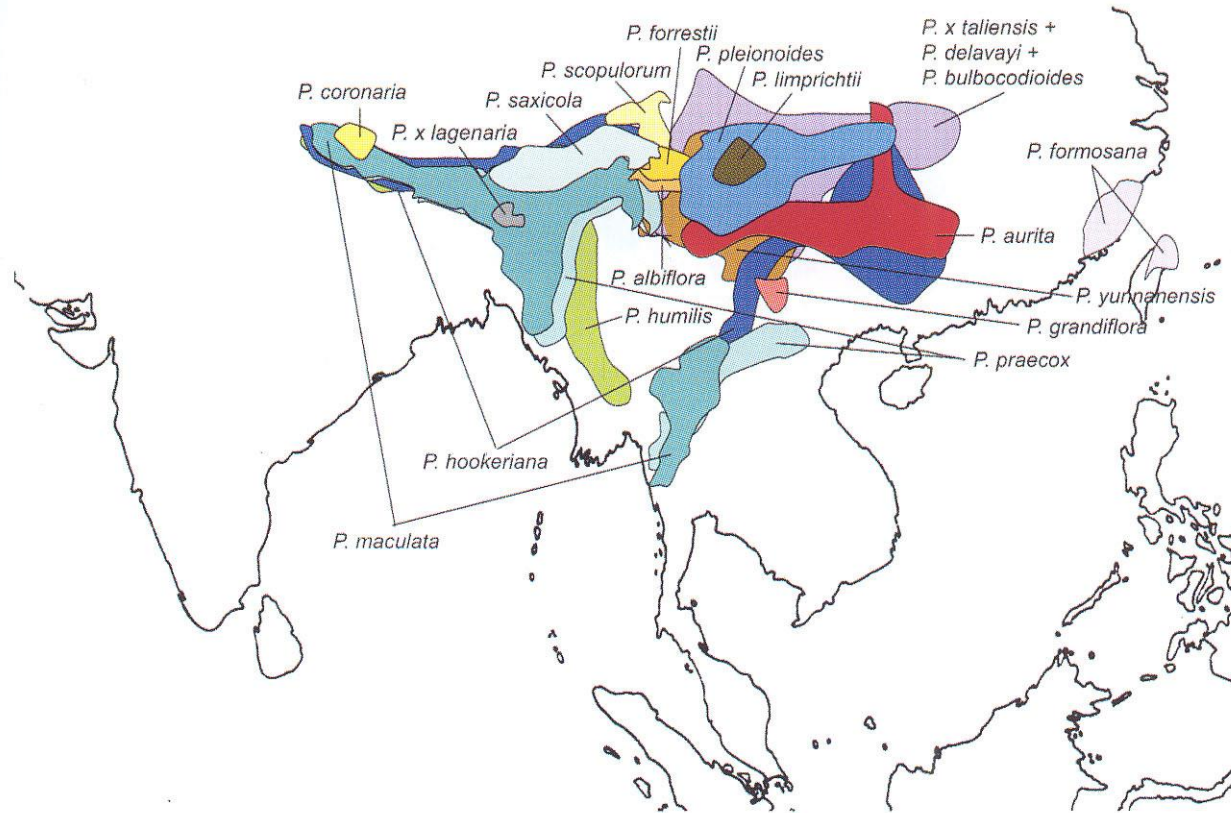
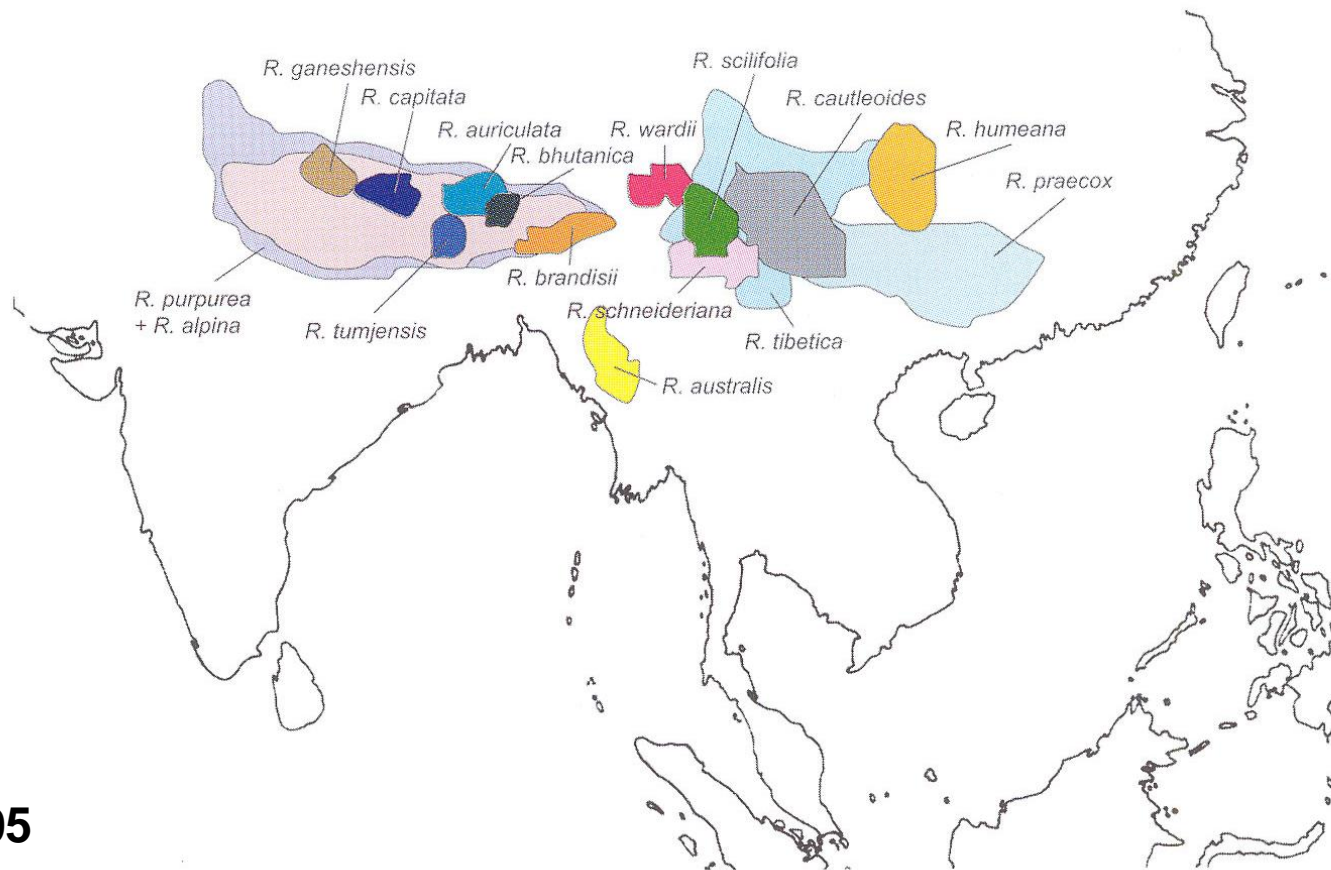


Fig. 4. Distribution maps of species of *Pleione* (Orchidaceae) included in this study. Note that areas are represented as overlapping, in case of disjunct distributions this is indicated here: *P. albiflora* (dark orange), *P. aurita* (dark red), *P. bulbocodioides* (light purple), *P. coronaria* (dark yellow), *P. delavayi* (light purple), *P. grandiflora* (light red), *P. hookeriana* (dark purple; disjunct), *P. humilis* (light green), *P. limprichtii* (black), *P. formosana* (pink; disjunct), *P. forrestii* (light orange), *P. x lagenaria* (dark grey), *P. maculata* (dark green; disjunct), *P. pleionoides* (dark blue), *P. praecox* (light blue; disjunct), *P. saxicola* (light grey), *P. scopulorum* (light yellow), *P. x taliensis* (light purple), and *P. yunnanensis* (brown). Data compiled from Cribb & Butterfield (1999) and Torelli (2000).



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Fig. 5. Distribution maps of species of *Roscoea* (Zingiberaceae) included in this study. Note that areas are indicated as overlapping: *R. alpina* (light pink), *R. auriculata* (dark green), *R. australis* (yellow), *R. brandisii* (dark orange), *R. bhutanica* (black), *R. capitata* (dark blue), *R. cautleoides* (dark grey), *R. ganeshensis* (dark brown), *R. humeana* (light orange), *R. praecox* (light grey), *R. purpurea* (light pink), *R. schneideriana* (light purple), *R. scillifolia* (light green), *R. tibetica* (light blue), *R. tumjensis* (dark pink) and *R. wardii* (red). Data compiled from Cowley (1982), Ngamriabsakul & al. (2000) and Ngamriabsakul & Newman (2000).

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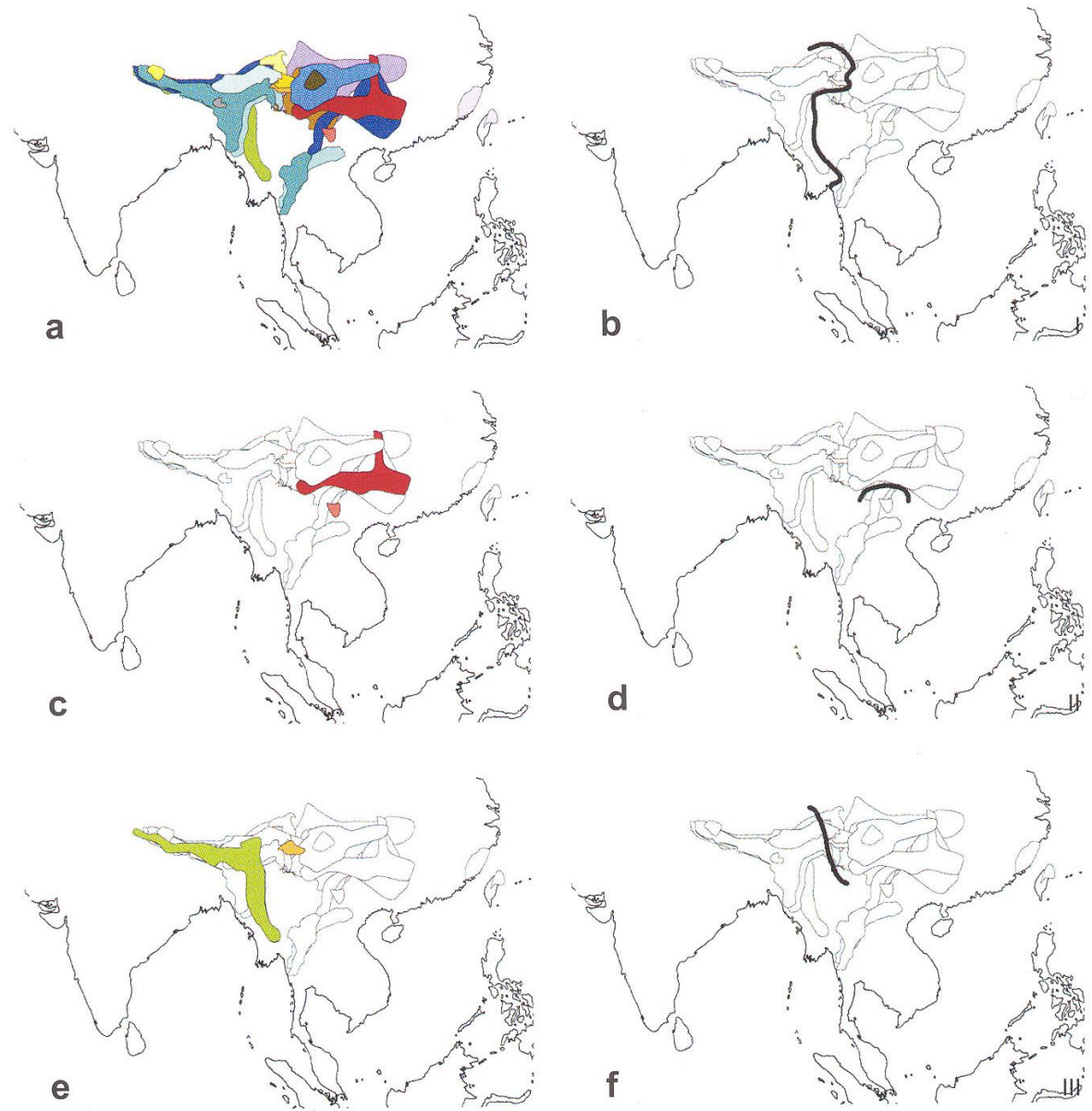


Fig. 6. Distribution maps for nodes 1–3 as indicated in Figs. 1c and 1d and the putative vicariance events I–III.

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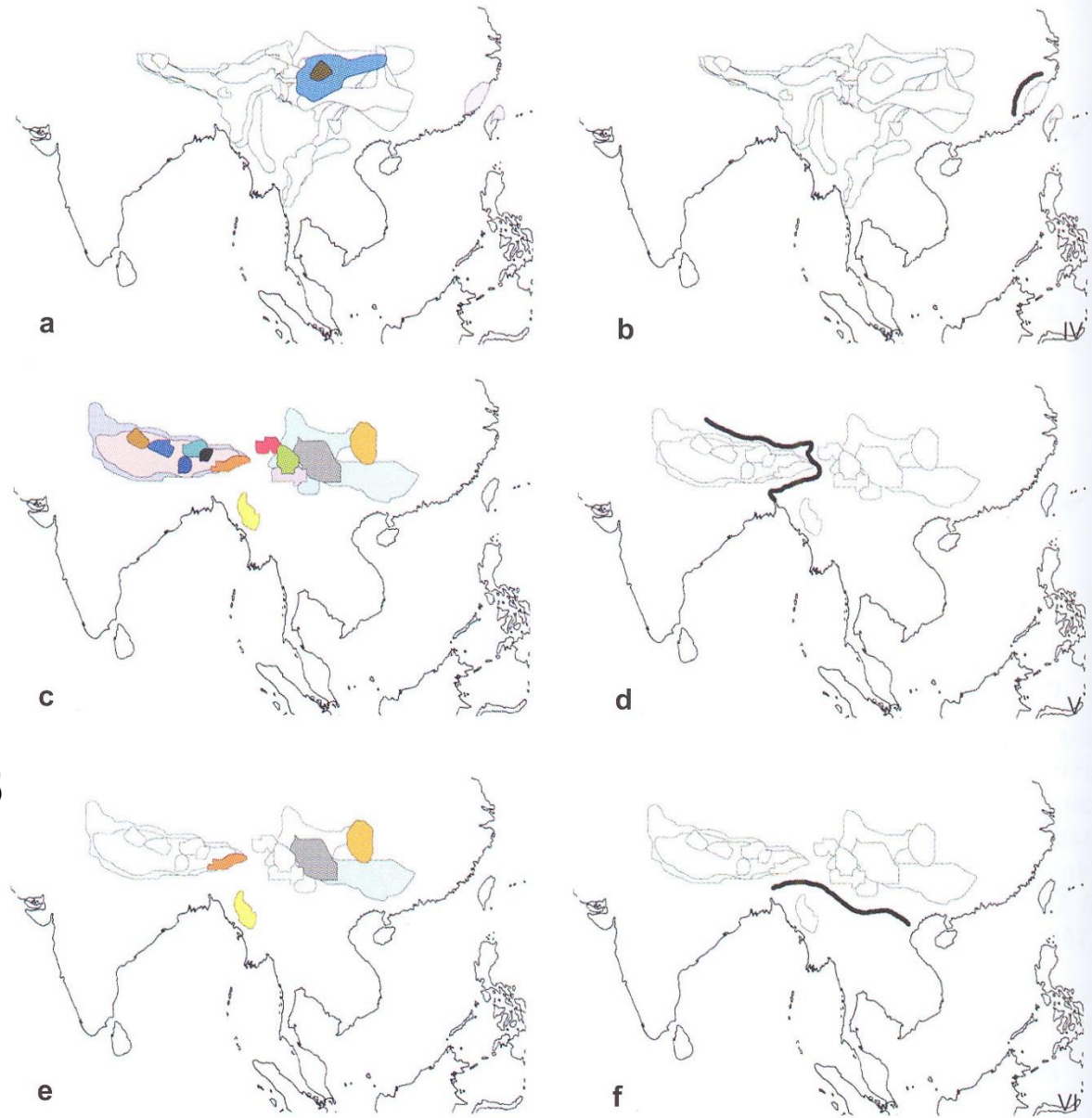


Fig. 7. Distribution maps for nodes 4–6 as indicated in Figs 1c and 1d and the putative vicariance events IV–VI.

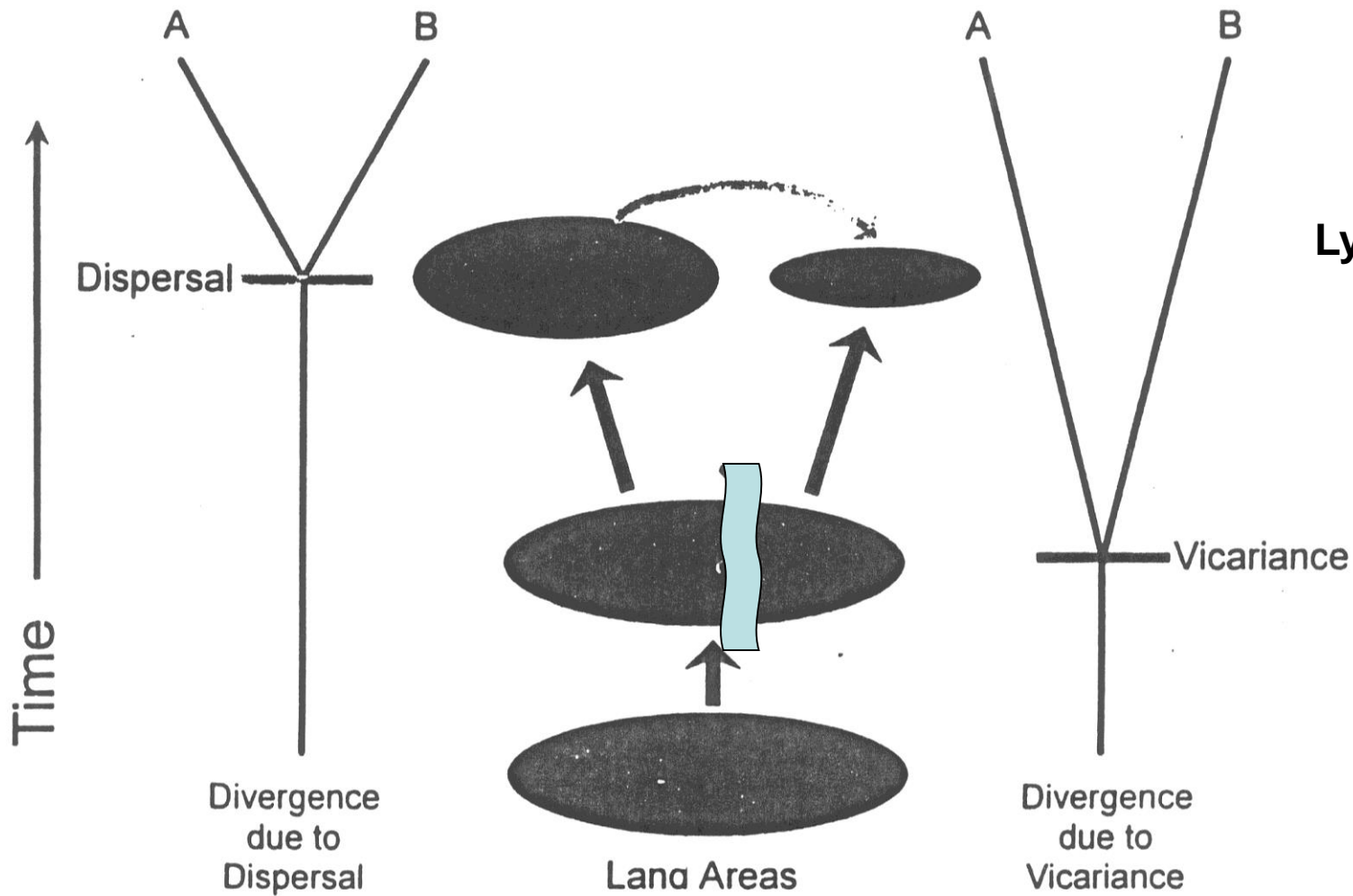


Fig. 1. Application of the time test in biogeographic analysis. Two groups on either side of a barrier are found to be sister taxa. Because the same phylogenetic relationships are expected with both models, examination of divergence times (through fossil evidence or molecular divergence) is necessary to distinguish between vicariance and dispersal. If the time of divergence between the two groups is shown to be significantly more recent than would be predicted by a vicariant event, then that vicariant event is rejected.

