
PARSIMONY ANALYSIS AND
CLADISTIC
RECLASSIFICATION OF THE
RELHANIA GENERIC GROUP
(ASTERACEAE–
GNAPHALIEAE)

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ABSTRACT

Parsimony analysis of the *Relhania* group of genera (Asteraceae–Gnaphalieae–Relhaniinae) yields a revised hypothesis of their phylogeny. The genera *Leysera* L. and *Oedera* L. are demonstrated to have their closest relatives within *Relhania* L'Hér., which is shown to be paraphyletic as hitherto circumscribed. A revised generic classification is proposed. *Relhania* and *Leysera* are redefined more narrowly. *Rhynchopsidium* DC. and the monotypic *Nestlera* Sprengel are reestablished. *Oedera* is amended to include some former *Relhania* species. The new genus *Comborhiza* Anderb. & Bremer, with 2 species, is described, and 14 new combinations in *Oedera* and *Comborhiza* are made. Because parsimony analysis produces better phylogenetic hypotheses than limited selections of alleged synapomorphies, and because the latter approach hitherto has been more common in generic classification, it is argued that, with improved phylogenetic hypotheses derived from parsimony analysis, generic reclassifications will become necessary also in other groups.

In this paper we present a parsimony analysis and propose a cladistic reclassification of a group of South African Asteraceae genera belonging to the tribe Gnaphalieae. The genera were revised during the 1970s and were then the subjects of some of the first cladistic approaches in botany (Bremer, 1976a, b, 1978a, b). At that time, uniquely derived, qualitative characters that could be interpreted as synapomorphies, unequivocally indicating monophyletic groups were sought. Thus, selected features, mainly of the pappus structure crowning the fruits, were used as putative synapomorphies defining the genera. Today, cladistics is methodologically much more sophisticated and is also considered a standard technique for analyzing phylogenies (Hull, 1989). Application of the parsimony criterion (Farris, 1983) in computerized programs has made it possible to use even large and homoplastic data sets including all kinds of information, minimizing a priori assumptions. Parsimony analysis of the *Relhania* group of genera yields a revised hypothesis of their phylogeny, and hence a basis for a cladistic reclassification.

It is not only the theoretical and methodological background to the study of the phylogeny that has changed during the past 15 years, but also the

knowledge of the phylogeny of the tribe Gnaphalieae as a whole (Anderberg, 1991). Furthermore, another genus, not considered in Bremer's 1976–1978 revisions, has recently been added to the group (Anderberg & Källersjö, 1988).

Bremer (1976a, b, 1978a, b) revised the taxonomy and nomenclature of the genera *Relhania*, *Rosenia*, *Leysera*, *Oreoleysera*, and *Antithrixia*. In trying to circumscribe correctly these genera as monophyletic groups, Bremer relied on particular characters as synapomorphies defining them. Thus, *Relhania*, with 29 species, was distinguished by its pappus of more or less connate scales and no bristles. Bremer also pointed out the hypothetical nature of the generic delimitation:

Admittedly the loss of pappus bristles might have occurred several times. However, since there is no evidence that *Relhania* should be polyphyletic in its present circumscription, I believe we must for the time being rely on this character as uniquely derived and keeping the genus together (Bremer 1976a: 9).

Relhania was amended by Bremer to include most of the species of the genus *Nestlera*, which prior to Bremer's work was used to house all the species with epaleate receptacles. Bremer showed

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that epaleate receptacles were not uniquely derived and could not be used to separate *Nestlera* from *Relhania*. Thus, Bremer (1976b) placed much of *Nestlera* in *Relhania* and transferred some species to *Rosenia*. The latter genus comprises four species and has a pappus of scales as well as 1–4 scabrid bristles.

Later, Bremer (1978a) revised the related genus *Leysera*. It has a pappus of scales and five mostly plumose bristles and was assumed to be monophyletic due to a synapomorphy in the very long peduncles. Again, Bremer commented on the pappus characters used to distinguish the three genera:

In *Leysera* the disc-floret pappus consists of scales and five (or sometimes fewer) bristles, in *Rosenia* it consists of scales and generally 1–2 bristles, and in *Relhania* there is a disc-floret pappus of scales only. In all three genera there are only scales and no bristles in the ray-floret pappus. These differences are rather slight and the derived conditions might conceivably have been reached more than once but there is no information indicating that the genera should be polyphyletic or paraphyletic. (Bremer 1978a: 371).

Bremer (1978b) also removed one former *Leysera* species with several pappus bristles and described it as the monotypic genus *Oreoleysera*. Another monotypic genus, *Antithrixia*, was noted as a close relative of *Relhania*, *Rosenia*, *Leysera*, and *Oreoleysera*.

Recently, Anderberg & Källersjö (1988) discussed the similarity between *Oedera* and some species of *Relhania*. A transfer of *Oedera*, which comprised six species, from the Anthemideae to the *Relhania* generic group was proposed. In a review of the tribe Gnaphalieae, Anderberg (1991) recognized the subtribe Relhaniinae comprising two major clades, viz. the *Metalasia* group, with 14 genera, and the *Relhania* group, with the genera *Relhania*, *Rosenia*, *Leysera*, *Oreoleysera*, *Antithrixia*, and *Oedera*. Anderberg considered *Oedera* to be the sister group of *Relhania*. However, no synapomorphy could be found to define *Relhania* if *Oedera* was kept separate. Intraspecific relationships between the two genera were not investigated, but the possibility that *Relhania* could be paraphyletic was noted.

Furthermore, Anderberg showed that the monotypic genus *Antithrixia* is the most plesiomorphic representative of the *Relhania* group. The other five genera share a synapomorphy in their pappus scales, absent in *Antithrixia* and the *Metalasia* group. (Bremer, (1978b) erroneously stated that *Oreoleysera* lacks pappus scales, which, albeit very narrow, do exist in *Oreoleysera*).

The presence of a monotypic genus as the sister

group of the rest of the *Relhania* group made an analysis of the entire *Relhania* group at the species level conceivable. Based on the characters presented in Tables 1 and 2, we have performed a parsimony analysis of the recognized species of the group, using *Antithrixia* as outgroup. The analysis and its taxonomic implications are presented below.

METHODS

DATA

The analysis was based mainly on the characters used by Bremer (1976a, b, 1978a, b) in his revisions. The character list has been amended with further characters by investigating the specimens housed in the Swedish Museum of Natural History (S). The characters are listed in Table 1. Only two species have not been available for study, viz. *Oedera muirii* and *Oedera laevis*. Most of the characters of *Oedera muirii* were possible to extract from the protologue of this species (Smith, 1927), but *Oedera laevis* has been omitted. However, judging from De Candolle's (1838) and Harvey's (1865) descriptions, it seems to be a typical representative of *Oedera*.

ANALYSIS

The data matrix in Table 2 was computed with a parsimony program (Hennig86, version 1.5) written by and obtained from J. S. Farris (1988), and using a standard PC-AT. The following options were used: multiple hennig (mhennig*, constructing several initial cladograms by adding the taxa of the character matrix in several different sequences, retaining the shortest cladogram of each) with a subsequent branch-breaker command (bb*, generating all the multiple, equally parsimonious cladograms that can be found). The cladograms were rooted with a hypothetical ancestor corresponding to the outgroup, *Antithrixia*. The multistate characters 13, 16, 29, and 45 were coded as additive (cc+) because the character states were hypothesized to represent a gradual transformation series. The characters 8, 21, 23, 43, and 46, on the other hand, were coded as nonadditive (cc-), since no such hypothesis could be formulated in these cases.

RESULTS

The analysis resulted in 200 equally parsimonious cladograms, each 123 steps long, with a consistency index (ci) of 0.45. One of these cladograms is shown in Figure 1. The strict consensus

TABLE 1. Characters used in the analysis of the *Relhania*-group. Plesiomorphic states are coded 0 and apomorphic states 1, 2, and 3 with *Antithrixia* as outgroup. See Methods for coding of multistate characters.

| | |
|-----|---|
| 1. | (0) Perennial half-shrubs or shrubs, (1) annual herbs. |
| 2. | (0) Subterranean woody rhizome absent, (1) subterranean woody rhizome present. |
| 3. | (0) Stem not subdichotomously branched, (1) stem subdichotomously branched. |
| 4. | (0) branches unarmed, (1) branches subspinescent or spinescent. |
| 5. | (0) Brachyblasts present, (1) brachyblasts absent. |
| 6. | (0) Leaves decussate, (1) leaves alternate. |
| 7. | (0) Leaves spreading, (1) leaves squarrose-recurved. |
| 8. | (0) Leaves linear-oblong, (1) leaves obovate-spathulate, (2) leaves widely cordate to orbicular. |
| 9. | (0) Leaf margin entire, smooth, (1) leaf margin apparently denticulate to sparsely serrate. |
| 10. | (0) Leaves blunt, (1) leaves pungent. |
| 11. | (0) Leaves mid-nerved, (1) leaves with at least three main nerves. |
| 12. | (0) Leaves adaxially more densely pubescent than abaxially, (1) leaves adaxially glabrous. |
| 13. | (0) Leaves glandular-hairy with stalked glands, (1) leaves glandular-punctate, (2) leaves glandular-punctate, with glands sunken in pits. |
| 14. | (0) Leaf margin not involute, (1) leaf margin involute. |
| 15. | (0) Capitula sessile or on short peduncles (generally <25 mm), (1) capitula on long peduncles (generally >25 mm). |
| 16. | (0) Capitula solitary, (1) capitula paired to cymose-corymbose or congested, (2) capitula many in dense secondary heads. |
| 17. | (0) Synflorescence not surrounded by a leafy involucre, (1) synflorescence surrounded by a leafy involucre. |
| 18. | (0) Involucral bracts with spreading limb, (1) involucral bracts with straight limb. |
| 19. | (0) At least some involucral bracts spathulate, (1) involucral bracts not spathulate. |
| 20. | (0) Receptacle without long squamae, (1) receptacle with long squamae. |
| 21. | (0) Receptacle naked, (1) receptacle paleate, with paleae abaxially to the florets, (2) receptacle deeply alveolate. |
| 22. | (0) Paleae deciduous, (1) paleae persistent. |
| 23. | (0) Paleae entire, (1) paleae apically serrate to lacinate, (2) paleae with two lateral teeth. |
| 24. | (0) Ray-florets monomorphic, (1) ray-florets dimorphic. |
| 25. | (0) Ray-floret lamina usually 4-veined, (1) ray-floret lamina frequently with up to 10 veins. |
| 26. | (0) Ray-floret tube cylindrical, (1) ray-floret tube somewhat triquetrous. |
| 27. | (0) Disc-florets perfect, (1) disc-florets functionally male, style undivided. |
| 28. | (0) Disc-floret corolla somewhat funnel-shaped, indistinctly divided in tube and limb, (1) disc-floret corolla distinctly divided in tube and limb. |

TABLE 1. Continued.

| | |
|-----|--|
| 29. | (0) Floret tubes eglandular or with few scattered glands, (1) floret tubes regularly glandular, (2) floret tubes with subulate-triangular hairs. |
| 30. | (0) Anther appendage acute to obtuse, (1) anther appendage truncate. |
| 31. | (0) Anther tails branched, (1) anther tails unbranched. |
| 32. | (0) Style branches in disc-florets apically penicillate, truncate, (1) style branches in disc-florets dorsally and apically penicillate, rounded-obtuse. |
| 33. | (0) Cypselas oblong-elliptic, (1) cypselas linear. |
| 34. | (0) Cypselas of ray-florets terete or angular, (1) cypselas of ray-florets sharply triquetrous. |
| 35. | (0) Cypselas of disc-florets terete or angular, (1) cypselas of disc-florets flattened. |
| 36. | (0) Cypselas glabrous, (1) cypselas at least in ray-florets pubescent. |
| 37. | (0) Cypselas of pubescent ray-florets pilose, (1) cypselas of pubescent ray-florets villose. |
| 38. | (0) Cypselas trichomes straight, (1) cypselas trichomes apically coiled. |
| 39. | (0) Cypselas generally eglandular, (1) cypselas regularly very glandular. |
| 40. | (0) Cypselas epidermis smooth, (1) cypselas epidermis with acute papillae. |
| 41. | (0) Cypselas with 5 vascular bundles (occasionally 10), (1) cypselas with 2-3 vascular bundles. |
| 42. | (0) Pappus bristles in ray-florets present, (1) pappus bristles in ray-florets absent. |
| 43. | (0) Pappus bristles in disc-florets numerous, (1) pappus bristles in disc-florets five, (2) pappus bristles in disc-florets one to four, (3) pappus bristles in disc-florets absent. |
| 44. | (0) Pappus bristles apically scabrid to barbellate, (1) pappus bristles apically plumose. |
| 45. | (0) Pappus scales free, (1) pappus scales connate, (2) pappus tubular. |
| 46. | (0) Basic chromosome number $x = 7$ ($2n = 14, 28, 56$), (1) basic chromosome number $x = 5$ ($2n = 10$), (2) basic chromosome number $x = 4$ ($2n = 8, 16$). |

tree in Figure 2 was computed with the nelsen option and shows the clades consistently present in all the equally parsimonious cladograms. In Figures 1 and 2 the terminal taxa are named as in Table 2, following the earlier generic classification, whereas the generic reclassification proposed below is indicated with names in capitals. In the following discussion, *Relhania* s.l., *Leysera* s.l., and *Oedera* s.s. refer to the earlier circumscriptions, whereas *Relhania* s.s., *Leysera* s.s., and *Oedera* s.l. refer to the proposed new delimitations.

Variation among the 200 equally parsimoniously cladograms is restricted to 100 alternative topologies within the screened right part of Figures 1 and 2 (*Oedera* s.l.) as well as to two alternative

TABLE 2. Data matrix. The characters are listed in Table 1. The taxon names follow the earlier classification. Inapplicable, unknown, or variable character states are coded -.

| | Character number | | | | | | | | | | | | | | | | | | | |
|-------------------------------|--|--|----------|------|--|--|--|--|--|--|--|--|--|--|--|--|--|--|--|--|
| | 0000000001111111111222222222233333333334444444 | 1234567890123456789012345678901234567890123456 | | | | | | | | | | | | | | | | | | |
| <i>Antithrixia flavicoma</i> | 00000000000000000000 | --000000000000000000 | 00000000 | -- | | | | | | | | | | | | | | | | |
| <i>Oreoleysera montana</i> | 000011010000001000100 | --0000010100001000000000 | 00000000 | -- | | | | | | | | | | | | | | | | |
| <i>Leysera longipes</i> | 010011000001001000000 | --00-0110101000--0001100- | | | | | | | | | | | | | | | | | | |
| <i>Leysera gnaphalodes</i> | 0000-1000000001000-10 | --00001211010010001111102 | | | | | | | | | | | | | | | | | | |
| <i>Leysera tenella</i> | 100011000000001000110 | --00001211010010001111102 | | | | | | | | | | | | | | | | | | |
| <i>Leysera leyseroides</i> | 100011000000001001110 | --00001211010010001111102 | | | | | | | | | | | | | | | | | | |
| <i>Rosenia glandulosa</i> | 00110000000000000000 | 10000000000000000000 | 10000000 | 201- | | | | | | | | | | | | | | | | |
| <i>Rosenia spinescens</i> | 00110000000000000000 | -000000000000000000 | 10000000 | 201- | | | | | | | | | | | | | | | | |
| <i>Rosenia oppositifolia</i> | 00000000000000000000 | --0000000-00001000000 | 2010 | | | | | | | | | | | | | | | | | |
| <i>Rosenia humilis</i> | 00-0000000-00000000 | -0000000000000000 | 1000000 | 2010 | | | | | | | | | | | | | | | | |
| <i>Relhania dieterlenii</i> | 000010000000110000000 | --0000100100000--00013-1- | | | | | | | | | | | | | | | | | | |
| <i>Relhania fruticosa</i> | 00001100000011000000 | 1000000100100000--00013-2- | | | | | | | | | | | | | | | | | | |
| <i>Relhania rotundifolia</i> | 00001101000011000000 | 1000100100100000--00013-2- | | | | | | | | | | | | | | | | | | |
| <i>Relhania spathulifolia</i> | 000011010000110000000000 | 11001000011000013-10 | | | | | | | | | | | | | | | | | | |
| <i>Relhania corymbosa</i> | 00001101000011010000000000 | 100100001100001301- | | | | | | | | | | | | | | | | | | |
| <i>Relhania tricephala</i> | 00001101000011010000000000 | 11001000011000013-10 | | | | | | | | | | | | | | | | | | |
| <i>Relhania relhanioides</i> | 00001101000011000000000000 | 11001000011000013-1- | | | | | | | | | | | | | | | | | | |
| <i>Relhania genistifolia</i> | 000011-00001100100001000000 | 11010000100-0013-10 | | | | | | | | | | | | | | | | | | |
| <i>Relhania viscosa</i> | 000011000001100100001000000 | 1101000010000013-10 | | | | | | | | | | | | | | | | | | |
| <i>Relhania squarrosa</i> | 000011100001100100001000000 | 1101010010000013-10 | | | | | | | | | | | | | | | | | | |
| <i>Relhania conferta</i> | 000011100001100100001000000 | 11010000--10113-1- | | | | | | | | | | | | | | | | | | |
| <i>Relhania steyniae</i> | 000010000101100100001000000 | 11010000--00013-10 | | | | | | | | | | | | | | | | | | |
| <i>Relhania garnotii</i> | 000011100000100100002--000111010000 | 11000113-10 | | | | | | | | | | | | | | | | | | |
| <i>Relhania multipunctata</i> | 000011000001200101001000000 | 110111000---0013-1- | | | | | | | | | | | | | | | | | | |
| <i>Relhania resinifera</i> | 000011000001200101101000000 | 1101000010000013-10 | | | | | | | | | | | | | | | | | | |
| <i>Relhania sedifolia</i> | 000011000001200101101000000 | 1101-10010000013010 | | | | | | | | | | | | | | | | | | |
| <i>Relhania foveolata</i> | 000011000001200000001000000 | 1001000010000013-1- | | | | | | | | | | | | | | | | | | |
| <i>Relhania nordenstamii</i> | 000000000001200101101000000 | 1101000010000013-1- | | | | | | | | | | | | | | | | | | |
| <i>Relhania uniflora</i> | 000010000001100000001000000 | 1101000010000013-10 | | | | | | | | | | | | | | | | | | |
| <i>Relhania silicicola</i> | 000010000001100100000--000011010000 | --10013-1- | | | | | | | | | | | | | | | | | | |
| <i>Relhania pumila</i> | 100011000000000000101020 | -001201000010100113-11 | | | | | | | | | | | | | | | | | | |
| <i>Relhania sessiliflora</i> | 100011000000000000101020000 | 1201000010100113-11 | | | | | | | | | | | | | | | | | | |
| <i>Relhania biennis</i> | 100011000000000000100--0-0012110100 | 10000013-21 | | | | | | | | | | | | | | | | | | |
| <i>Relhania tuberosa</i> | 010001000001000000000000000 | 1101000010000113-10 | | | | | | | | | | | | | | | | | | |
| <i>Relhania acerosa</i> | 001011000101100000000--000011011100 | 10000113-1- | | | | | | | | | | | | | | | | | | |
| <i>Relhania decussata</i> | 0000100001001000000011000001001100 | 100010000113-10 | | | | | | | | | | | | | | | | | | |
| <i>Relhania pungens</i> | 000011000110000000001100-100200 | 101110000113-10 | | | | | | | | | | | | | | | | | | |
| <i>Relhania calycina</i> | 000011-00111000000001100-100200 | 101110000113-10 | | | | | | | | | | | | | | | | | | |
| <i>Relhania speciosa</i> | 000011-00111-000000011001100200 | -01110000113-10 | | | | | | | | | | | | | | | | | | |
| <i>Oedera capensis</i> | 000011101101000210001011100120 | 100000--00013-1- | | | | | | | | | | | | | | | | | | |
| <i>Oedera hirta</i> | 000011121111000210001011100110 | 100000--00013-1- | | | | | | | | | | | | | | | | | | |
| <i>Oedera imbricata</i> | 000011121111000210001011100120 | 100000--00013-1- | | | | | | | | | | | | | | | | | | |
| <i>Oedera intermedia</i> | 000011101111000210001011100120 | 100000--00013-10 | | | | | | | | | | | | | | | | | | |
| <i>Oedera muirii</i> | 000010101111000210001011100100 | 100000--00-13-1- | | | | | | | | | | | | | | | | | | |

sister groups to *Relhania tricephala*, either *R. corymbosa* or the species pair *R. relhanioides* + *R. spathulifolia*, within the screened left part of Figures 1 and 2 (*Relhania* s.s.). The majority of the clades in the cladogram in Figure 1 are present in all the other equally parsimonious cladograms, as shown by the strict consensus tree in Figure 2.

Several analyses were also performed with slight modifications of the data matrix, omitting some characters or including others not accepted in the final matrix (ultimately rejected for various reasons, for example, because of unreliable information in some taxa or because of strong correlation with other included characters such as presence of

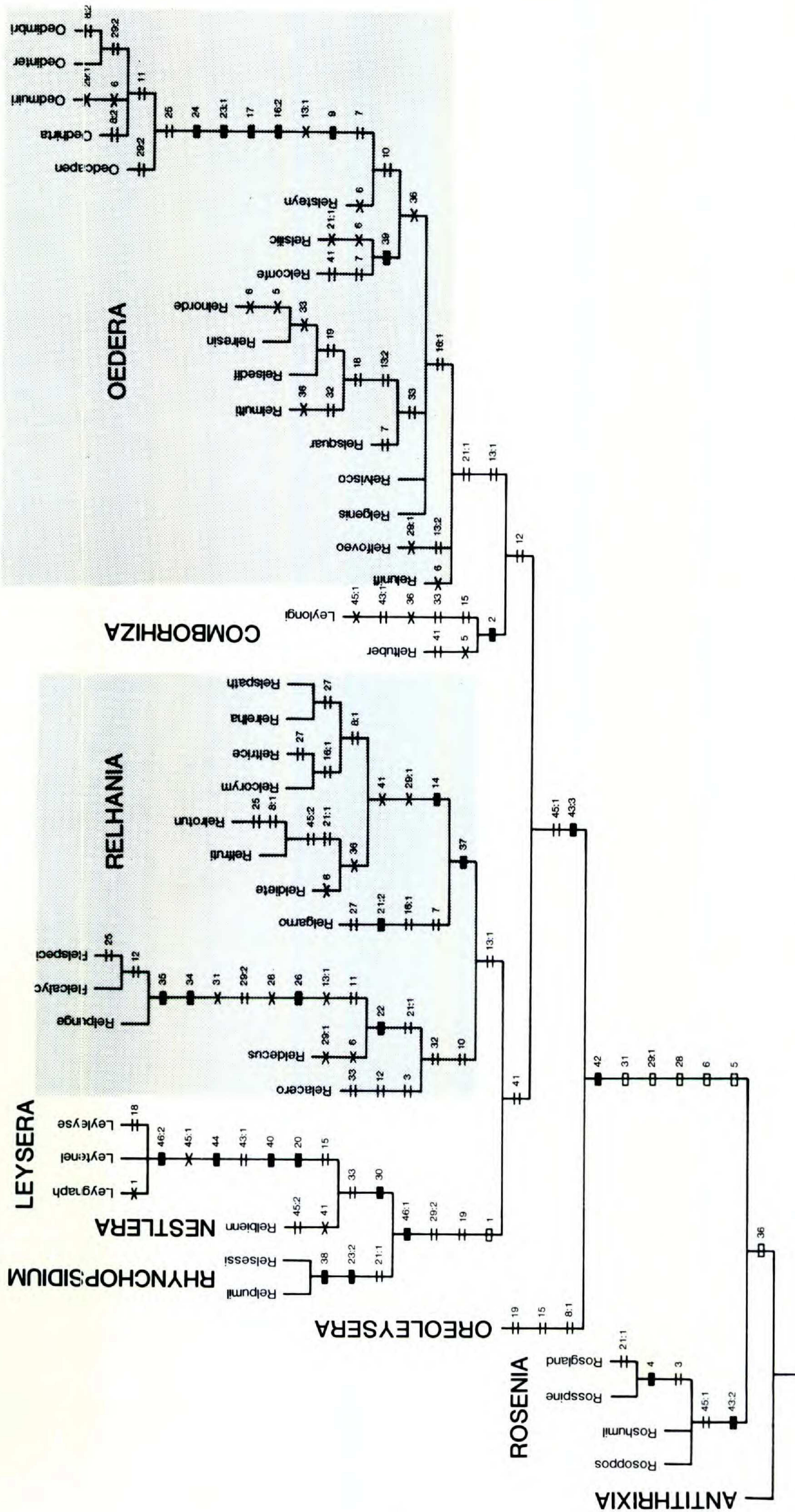


FIGURE 1. One of the 200 equally parsimonious cladograms obtained from analysis of the data matrix in Table 2. Black squares = synapomorphies, open squares = synapomorphy with reversals on the cladogram, crosses = reversals, parallel lines = parallelisms. The numbers correspond to the characters in Table 1. Terminal taxon names as in Table 2, following the earlier generic classification. Proposed new generic classification in capitals.

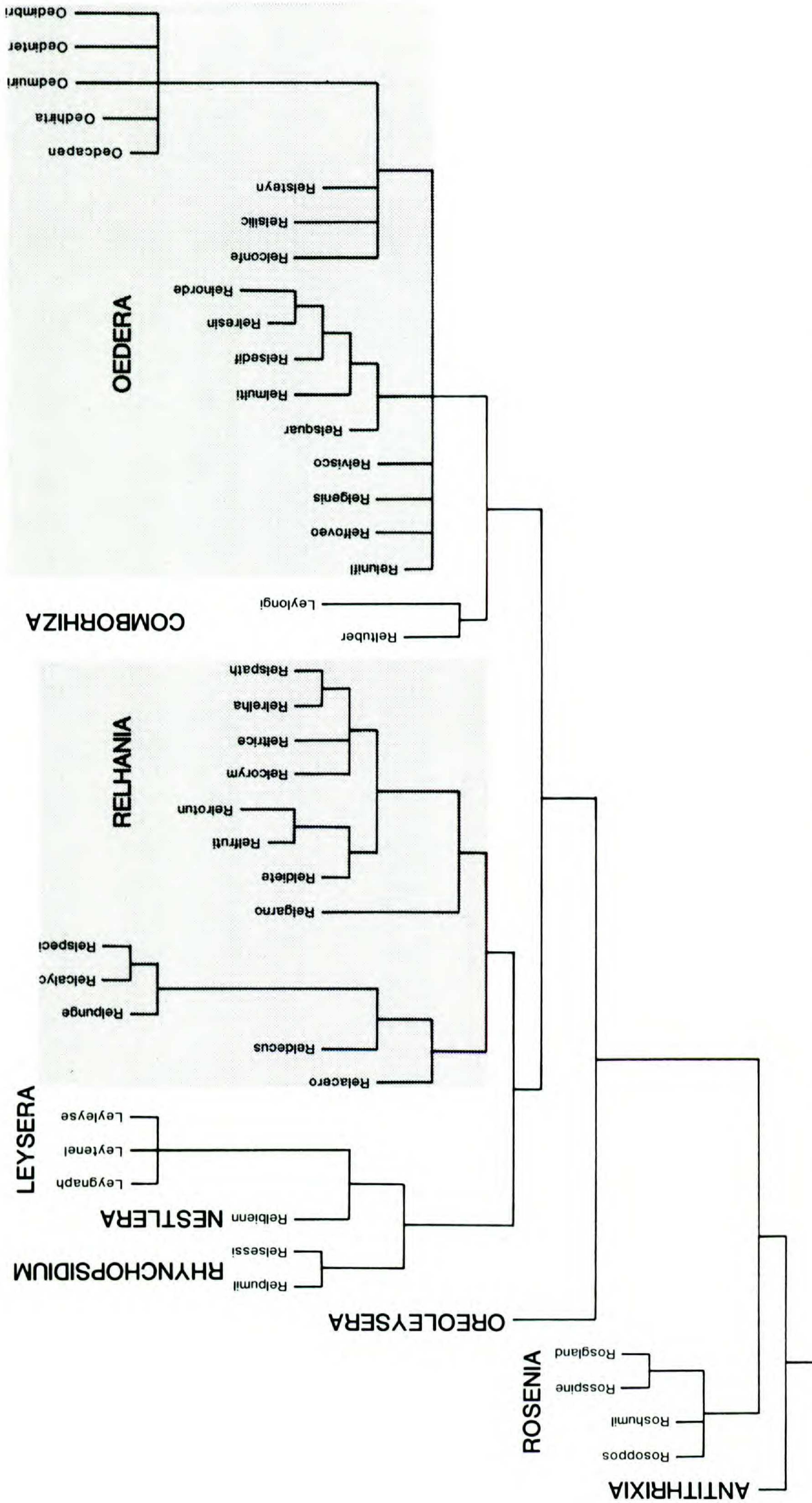


FIGURE 2. Strict consensus tree based on all the 200 equally parsimonious cladograms obtained from analysis of the data matrix in Table 2. Terminal taxon names as in Table 2, following the earlier generic classification. Proposed new generic classification in capitals. Shaded areas show the circumscription of *Relhania* and *Oedera*, respectively.

glands on various organs). These analyses showed, as might be expected, that the clades supported by single parallelisms are weak and easily broken up even with slight changes in the data matrix. However, in all analyses, *Rosenia* and *Oreoleysera* successively came out at the base of the cladogram with the remaining genera as one monophyletic group. Furthermore, *Leysera* and *Oedera* were always firmly nested within a paraphyletic *Relhania* s.l.

DISCUSSION

The consistency index 0.45 and the frequent occurrence of parallelisms and reversals on the cladogram in Figure 1 show that there is considerable homoplasy in the data, as is usually found in similarly sized analyses of other groups. The impact of homoplastic characters on the phylogenetic hypothesis is important, and the most parsimonious way in which these characters can be distributed on a cladogram is virtually impossible to detect without computerized programs. As a scientific theory, the phylogeny reconstructed by parsimony analysis is superior to any phylogeny obtained from a limited selection of characters only, since the former takes into account all available information. Parsimony analysis is increasingly employed in taxonomic revisions, and it offers possibilities for improved, phylogenetically more informative classifications, where the named taxa reflect evolutionary units rather than artificially composed groups defined only by a few characters.

In this case, the analysis clearly demonstrates that *Relhania* s.l. is paraphyletic with *Leysera* and *Oedera* excluded. Delimitation among the three genera has to be altered in order to meet the demand for monophyletic taxa. To lump all genera into a single genus, *Leysera* sensu latissimo (*Leysera* being the oldest name), would result in a very heterogeneous taxon, defined only by characters such as absence of brachyblasts, alternate leaves, glandular floret tube, unbranched anther tails, ray-florets without pappus, and corolla divided in tube and limb. The characters are weak and can, in a wider context, also be shown to be parallelisms (e.g., by investigation of a larger number of taxa of the Gnaphalieae). A better alternative is to split *Relhania* and *Leysera* and recognize smaller monophyletic genera that are more morphologically homogeneous. This would mean the separation of the apomorphic *Leysera* s.s., *Rhynchopsidium*, *Comborhiza*, and *Oedera* from each other, and from *Relhania*. The definition of *Oedera* is hereby weakened due to the transfer to this genus

of 10 *Relhania* species. This is unfortunate, but no other alternative is at hand if we want to maintain monophyletic genera. *Relhania* itself is poorly defined but still constitutes a monophyletic group. By accepting this second classification, we gain a detailed, predictive phylogenetic hypothesis with more explanatory power, because more taxonomic statements are made. To reduce all this information of phylogenetic interrelationships and conceal it in a lumping such as outlined above would hardly improve scientific progress.

Consequently, we have resurrected *Nestlera* in its original monotypic sense, reestablished the old ditypic genus *Rhynchopsidium*, described another ditypic genus *Comborhiza*, and transferred a number of the former *Relhania* species to *Oedera* (see Figs. 1, 2).

Relhania is restricted to 13 species, mostly with hairy and glandular-punctate (not glandular-hairy) leaves and solitary capitula. The genus comprises two distinct groups, recognized also by Bremer (1976a), as well as a more isolated species, *R. garnotii*. The two groups are *R. acerosa* to *R. speciosa*, with five species (including the distinct subgroup comprising *R. pungens*, *R. calycina*, and *R. speciosa*), and *R. dieterlenii* to *R. spathulifolia*, with seven species (see Figs. 1, 2).

Leysera is restricted to the three typical species and is thus the most well-defined of all the genera, with a whole set of synapomorphies, e.g., plumose pappus bristles (see Fig. 1). The former *Leysera longipes* and *Relhania tuberosa* are grouped as sister species in the new genus *Comborhiza*. They have a unique synapomorphy in their thick subterranean rhizomes. Although different in several characters, the two species are habitually similar, *Comborhiza virgata* (= *Relhania tuberosa*) having pedunculoid stems with reduced leaves beneath the capitula, approaching the condition in *C. longipes*. The genus has adaxially glabrous, dorsally glandular-hairy leaves, not glandular-punctate as in *Relhania* s.s. and *Oedera* s.l.

The monotypic genus *Nestlera* and the ditypic genus *Rhynchopsidium* are successive sister groups to *Leysera* s.s. (see Figs. 1, 2). Except for the (secondarily) perennial *L. gnaphalodes*, they are annuals or biennials with reduced chromosome base numbers, $x = 5$ in *Rhynchopsidium* and *Nestlera*, and $x = 4$ in *Leysera*. (Humphries et al. (1978) reported $2n = 14$ for *L. leyseroides*, a count that must be doubted in the light of Blanca's (1983) detailed investigation of the karyology of the species; Blanca showed that *L. leyseroides* is a tetraploid with $2n = 16$.)

Oedera, finally, is amended to include 12 former

Relhania species, and as such *Oedera* s.l. is characterized by the generally glabrous, glandular-punctate leaves, and the cymose-corymbose to congested capitula. Intraspecific relationships within *Oedera* are still uncertain. The analysis produced 100 equally parsimonious topologies within *Oedera* s.l. Nevertheless, it must be concluded that *Oedera* s.s. is firmly nested within the larger monophyletic group that we have circumscribed as *Oedera* s.l. Hence, *Oedera* s.s. cannot be maintained at the generic level, since it would leave an unresolved paraphyletic residue of former *Relhania* species.

CONCLUSION

The former generic classification of the *Relhania* group was based on selected, alleged syn-

apomorphies, the usual cladistic approach during the middle-1970s. Thus, Bremer (1976a, 1978a) defined genera on some pappus features, at the same time pointing out the possibility that the supposed synapomorphies could be false. Parsimony analysis of all the characters has indeed produced a revised picture of the phylogeny. We have re-circumscribed genera according to the best phylogenetic hypothesis available, as expressed in the cladograms produced by the analysis. Reclassification of genera like *Relhania* s.l., formerly defined by unique, alleged synapomorphies, which in parsimony analysis of larger groups are shown to be false, is likely to become necessary in many other generic groups as well.

The present classification of the *Relhania* group is summarized in the following key:

- 1a. Plants compact, cushion-forming *Oreoleysera*
- 1b. Plants not cushion-forming.
 - 2a. Pappus of capillary bristles, scales absent *Antithrixia*
 - 2b. Pappus at least in ray-florets with conspicuous scales, bristles present or absent.
 - 3a. Pappus bristles distinctly plumose *Leysera*
 - 3b. Pappus bristles scabrid-barbellate or absent.
 - 4a. Annual or biennial herbs.
 - 5a. Cypselas densely hairy with long, apically coiled hairs *Rhynchopsidium*
 - 5b. Cypselas almost glabrous *Nestlera*
 - 4b. Perennial half-shrubs, shrublets or shrubs.
 - 6a. Disc-florets with 1-4 pappus bristles *Rosenia*
 - 6b. Disc-florets without pappus bristles.
 - 7a. Plants glabrous (if hairy then with capitula congested in secondary heads), capitula generally cymose-corymbose to clustered in secondary heads (if solitary then with glabrous, \pm distinctly one-nerved leaves) *Oedera*
 - 7b. Plants \pm hairy or glandular-hairy (if glabrous then with distinctly 3-9-nerved leaves), capitula generally solitary (if corymbose then with hairy leaves).
 - 8a. Leaves with long glandular hairs *Comborhiza*
 - 8b. Leaves without long glandular hairs *Relhania*

Antithrixia DC., Prodr. 6: 277. 1838. TYPE: *A. flavicoma* DC.

Shrublet. *Leaves* opposite or crowded on brachyblasts, sessile, linear, adaxially concave and tomentose, glandular-hairy, apically mucronate; margin entire. *Capitula* solitary, terminal, heterogamous, radiate. Involucral bracts with spatulate laminae. *Receptacle* flat, epaleate. *Female florets* yellow with purple bands dorsally, pistillate, radiate, in one row, fewer than the disc-florets. *Cypselas* and pappus as in disc-florets. *Disc-florets* perfect. Corolla yellow. Anthers ecalcarate with short tails; endothelial tissue polarized; apical appendage acute. Style branches truncate with obtuse sweeping-hairs apically. *Cypselas* rodlike, with ten (2×5) vascular bundles, glabrous or with a few scattered, elongated twin hairs. Pappus of slightly

connate, barbellate, capillary bristles in one to two rows. *Chromosome number* unknown.

Monotypic: *A. flavicoma* DC. Reference: Bremer, 1978b.

Rosenia Thunb., Nov. Gen. 161. 1800. TYPE: *R. glandulosa* Thunb.

Synonym: *Polychaetia* Less.

Shrublets. *Leaves* decussate or rarely alternate, straight, adaxially concave, tomentose, glandular-hairy; margin entire. *Capitula* heterogamous, radiate, solitary or few together. Involucral bracts with spatulate laminae. *Receptacle* flat, often paleate. *Female florets* yellow with purple bands dorsally, radiate, pistillate, in one row, fewer than the disc-florets. *Cypselas* and pappus as in disc-florets.

Disc-florets perfect. Corolla yellow. Anthers ecalcarate with short tails; endothelial tissue polarized; apical appendage acute. Style branches \pm truncate with obtuse sweeping-hairs apically. *Cypselas* rod-like with five vascular bundles, sparsely hairy with elongated twin hairs. Pappus a crown of \pm free scales, and 1–4, barbellate, capillary bristles with flattened apical portion. *Chromosome number* $2n = 14, 28, 56$.

Four species: *R. glandulosa* Thunb., *R. humilis* (Less.) Bremer, *R. oppositifolia* (DC.) Bremer, *R. spinescens* DC. Reference: Bremer, 1976b.

Oreoleysera Bremer, Bot. Not. 131: 450. 1978.

TYPE: *O. montana* (Bolus) Bremer.

Compact woody perennial, forming dense tufts. *Leaves* alternate, sessile, narrowly oblong, flattened, grayish tomentose on both surfaces, eglandular; margin entire. *Capitula* solitary, terminal on long leafless peduncles, heterogamous, radiate. Involucral bracts with lanceolate laminas. *Receptacle* flat, epaleate. *Female florets* yellow with purple bands dorsally, pistillate, radiate, in one row, fewer than the disc-florets. *Cypselas* and pappus as in disc-florets. *Disc-florets* perfect. Corolla yellow, glandular-hairy. Anthers ecalcarate with short tails; endothelial tissue polarized; apical appendage acute. Style branches truncate with obtuse sweeping hairs apically. *Cypselas* rodlike with five vascular bundles, moderately hairy with elongated twin hairs. Pappus of free, barbellate, capillary bristles in one row with an outer row of very narrow scales. *Chromosome number* unknown.

Monotypic: *O. montana* (Bolus) Bremer. Reference: Bremer, 1978b.

Rhynchopsidium DC., Mém. Soc. Phys. Genève 7: 283. 1836. TYPE: *R. sessiliflorum* (L. f.) DC.

Synonym: *Rhynchocarpus* Less., nom. illeg.

Annual herbs. *Leaves* alternate or sometimes opposite, straight, adaxially concave, tomentose, glandular-hairy; margin entire. *Capitula* heterogamous, radiate, solitary, sessile or pedunculate. Involucral bracts with lanceolate laminas. *Receptacle* flat-convex, paleate; paleae lanceolate with two lateral teeth. *Female florets* yellow with purple bands dorsally, radiate, pistillate, in one row, fewer than the disc-florets. *Cypselas* and pappus as in disc-florets. *Disc-florets* perfect. Corolla yellow, often with robust multicellular trichomes. Anthers

ecalcarate, with short tails; endothelial tissue polarized; apical appendage acute. Style branches truncate with obtuse sweeping-hairs apically. *Cypselas* narrowly elliptic with three vascular bundles, densely hairy with elongated, apically coiled twin hairs. Pappus a crown of \pm free scales. *Chromosome number* $2n = 10$.

Two species: *R. pumilum* (L. f.) DC. (= *Relhania pumila* (L. f.) Thunb.), *R. sessiliflorum* (L. f.) DC. (= *Relhania sessiflora* (L. f.) Thunb.). Reference: Bremer 1976a (spp. 21–22).

Nestlera Sprengel, Anleit. Kennt. Gewächse 2(2): 568. 1818. TYPE: *N. biennis* (Jacq.) Sprengel.

Synonyms: *Columellea* Jacq. nom. illeg., *Stephanopappus* Less.

Biennial herb. *Leaves* alternate or occasionally opposite, straight, adaxially concave, tomentose, glandular-hairy; glands with multicellular heads; margin entire. *Capitula* heterogamous, radiate, solitary or few together. Involucral bracts with lanceolate laminas. *Receptacle* flat, often paleate. *Female florets* yellow with purple bands dorsally, radiate, pistillate, in one row, fewer than the disc-florets. *Cypselas* and pappus as in disc-florets. *Disc-florets* perfect. Corolla yellow, often with robust multicellular trichomes. Anthers ecalcarate, with short tails; endothelial tissue polarized; apical appendage truncate. Style-branches \pm truncate with obtuse sweeping-hairs apically. *Cypselas* rodlike with five vascular bundles, sparsely hairy with elongated twin hairs. Pappus a tubular crown of connate scales. *Chromosome number* $2n = 10$.

Monotypic: *N. biennis* (Jacq.) Sprengel (= *Relhania biennis* (Jacq.) Bremer). Reference: Bremer, 1976a (sp. 23).

Leysera L. Sp. Pl. ed. 2, 2: 1249, 1763; Amoen. Acad. 6: 104, 1763; Gen. Pl. ed. 6: 431, 1764. TYPE: *L. gnaphalodes* (L.) L.

Synonyms: *Asteropterus* (Vaill.) Adans., *Callicornia* Burm. f., *Callisia* L., *Leptophytus* Cass., *Longchampia* Willd., *Pseudocrupina* Velen., *Leyseria* Necker, *Leyssera* auct., ortogr. var.

Annual herbs or a perennial half-shrub or shrublet. *Leaves* alternate or occasionally opposite, sessile, linear, straight, mucronate, adaxially concave, tomentose, glandular-hairy; margin entire. *Capitula* heterogamous, radiate, solitary, terminal on long leafless peduncles. Involucral bracts with lanceolate laminas. *Receptacle* flat, marginally with prominent squamae. *Female florets* yellow with

purple bands dorsally, radiate or miniradiate, pistillate, in one row, fewer than the disc-florets; tube often with robust, conical trichomes. *Cypselas* as in disc-florets. Pappus of scales only. *Disc-florets* perfect. Corolla yellow, often with robust multicellular trichomes. Anthers ecalcarate, with short tails; endothelial tissue polarized; apical appendage truncate. Style branches truncate with obtuse sweeping-hairs apically. *Cypselas* rodlike, with three vascular bundles, glabrous or with scattered, elongated twin hairs. Pappus of free, apically plumose, capillary bristles in one row with an outer row of obtuse scales. *Chromosome number* $2n = 8, 16$.

Three species: *L. gnaphalodes* (L.) L., *L. leyseroides* (Desf.) Maire, *L. tenella* DC. Reference: Bremer, 1978a.

Relhania L'Hér., nom. cons.. Sert. Angl. 1: 22, 1789. TYPE: *R. fruticosa* (L.) Bremer.

Synonyms: *Osmites* L., *Lapeirousia* Thunb., nom. illeg.

Shrubs, shrublets, or half-shrubs. *Leaves* alternate or decussate, sessile, straight, adaxially concave, tomentose, margin entire. *Capitula* heterogamous, radiate, solitary or sometimes cymose-corymbose. Involucral bracts with spathulate laminae. *Receptacle* flat to convex or rarely deeply alveolate, often paleate. *Female florets* yellow with purple bands dorsally, radiate, pistillate, in one row, fewer than the disc-florets. *Cypselas* and pappus as in disc-florets. *Disc-florets* perfect or functionally male. Corolla yellow, sometimes with robust multicellular trichomes. Anthers ecalcarate, with short tails; endothelial tissue polarized; apical appendage acute. Style branches truncate with obtuse sweeping-hairs apically (rarely obtuse with sweeping-hairs dorsally). *Cypselas* rodlike with 5 or 3 vascular bundles, glabrous or sparsely hairy with elongated twin hairs. Pappus a crown of free to connate scales without bristles, occasionally with 1 or 2 barbellate bristles in odd florets. *Chromosome number* $2n = 14$.

Thirteen species: *R. acerosa* (DC.) Bremer, *R. calycina* (L. f.) L'Hér., *R. corymbosa* (Bolus) Bremer, *R. decussata* L'Hér., *R. dieterlenii* (E. Phillips) Bremer, *R. fruticosa* (L.) Bremer, *R. garnotii* (Less.) Bremer, *R. pungens* L'Hér., *R. relhaniaioides* (Schltr.) Bremer, *R. rotundifolia* Less., *R. spathulifolia* Bremer, *R. speciosa* (DC.) Harv., *R. tricephala* (DC.) Bremer. Reference: Bremer, 1976a (spp. 1-7, 13, 25-29).

Comborhiza Anderb. & Bremer, gen. nov. TYPE:

C. virgata (N. E. Br.) Anderb. & Bremer. Eponymy: The name is deduced from the Greek words *combos*, meaning knot, tuber, and *rhiza*, meaning root.

Fruticulus vel suffrutex. Caules rhizomate vel tubere hypogaeo, crasso, lignoso exorientes. *Folia* alterna vel in brachyblastis congesta, sessilia, stricta, concava, inferne glandulis longistipitatis praedita, superne glabra, margine integra. *Capitula* heterogama, radiata, solitaria, ad apices caulium paucifoliorum vel pedunculorum longissimorum. Bracteae involucri pluriseriatae lamina scariosa, spathulata infuscata. *Receptaculum* planum vel convexum, epaleatum. *Flosculi radii* flavi sed dorso interdum purpureo-fasciati, pistillati, uniseriati, flosculos disci pauciores. *Cypselae* eadem in flosculis disci. Pappus ex squamis angustis scariosis constans. *Flosculi disci* perfecti. Corolla flava. Antherae ecalcaratae, breviter caudatae, appendicibus apicalibus acutis; endothecio polarato. Styli rami apice truncati, pilis obtusis apicaliter. *Cypselae* anguste ellipticae, tri- vel quinquevenosae, pilosae vel fere glabrae. Pappus ex setis liberis, capillaribus, barbellatis, uniseriatis et squamis angustis scariosis vel tantum squamis scariosis plus minusve connatis solum constans.

Shrublet or suffrutex. Stems arising from subterranean, thick woody tubers or rhizomes. *Leaves* alternate or crowded on brachyblasts, sessile, straight, adaxially concave, glabrous above, glandular-hairy below, margin entire. *Capitula* heterogamous, radiate, solitary, on pedunculoid few-leaved stems or on long leafless peduncles. Involucral bracts with spathulate laminae. *Receptacle* flat or flat to convex, epaleate. *Female florets* yellow with purple bands dorsally, radiate, pistillate, in one row, fewer than the disc-florets. *Cypselas* as in disc-florets. Pappus of narrow scales. *Disc-florets* perfect. Corolla yellow. Anthers ecalcarate, with short tails; endothelial tissue polarized; apical appendage acute. Style branches truncate with obtuse sweeping-hairs apically. *Cypselas* narrowly elliptic with five or three vascular bundles, glabrous or sparsely hairy with elongated twin hairs. Pappus of 5 barbellate capillary bristles and narrow scales, or of \pm connate scales only. *Chromosome number* $2n = 14$.

Two species:

C. longipes (Bremer) Anderb. & Bremer, comb. nov. Basionym: *Leysera longipes* Bremer, Bot. Not. 131: 381. 1978.

C. virgata (N. E. Br.) Anderb. & Bremer, comb. nov. Basionym: *Nestlera virgata* N. E. Br., Kew Bull. 1895: 25 (= *Relhania tuberosa* Bremer).

References: Bremer, 1976a (sp. 24), 1978a (sp. 4).

Oedera L., nom. cons. emend. Anderb. & Bremer, emend nov. Mant. Pl. 159, 1771. TYPE: *O. capensis* (L.) Druce.

Synonyms: *Eroeda* Levyns, nom. illeg., *Eclopes* Gaertner.

Shrubs or shrublets. *Leaves* alternate or decussate, ovate to linear, mucronate, adaxially concave, glabrous or sometimes sparsely pilose, glandular; margin entire but sometimes provided with prominent, robust teethlike hairs. *Capitula* generally densely cymose-corymbose or even forming secondary heads surrounded by a common involucre of leaves, heterogamous, radiate, few-flowered. Involucral bracts with spatulate laminas. *Receptacle* flat to conical-convex, paleate or occasionally epaleate. *Female florets* yellow with purple bands dorsally, radiate in some species miniradiate or almost tubular in different positions in the head, in one row, fewer than the disc-florets. *Cypselas* and pappus as in disc-florets. *Disc-florets* perfect. Corolla yellow, sometimes with robust multicellular trichomes. Anthers ecalcarate, with short tails; endothelial tissue polarized; apical appendage acute. Style branches generally truncate with obtuse sweeping-hairs apically. *Cypselas* rodlike, with 5 vascular bundles, glabrous or with a few elongated twin hairs. Pappus a crown of \pm connate scales, without bristles. *Chromosome number* $2n = 14$.

Eighteen species:

- O. capensis* (L.) Druce, *O. hirta* Thunb., *O. imbricata* Lam., *O. intermedia* DC., *O. laevis* DC., *O. muirii* C. A. Smith.
O. conferta (Hutch.) Anderb. & Bremer comb. nov. Basionym: *Relhania conferta* Hutch., Ann. S. African Mus. 9: 381. 1917.
O. foveolata (Bremer) Anderb. & Bremer, comb. nov. Basionym: *Relhania foveolata* Bremer, Opera Bot. 40: 52. 1976.
O. genistifolia (L.) Anderb. & Bremer, comb. nov. Basionym: *Athanasia genistifolia* L., Syst. Nat. 2 Ed. 12: 540. 1767 (= *Relhania genistifolia* (L.) L'Hér.).
O. multipunctata (DC.) Anderb. & Bremer, comb. nov. Basionym: *Relhania multipunctata* DC., Prodr. 6: 286, 1838.
O. nordenstamii (Bremer) Anderb. & Bremer, comb. nov. Basionym: *Relhania nordenstamii* Bremer, Opera Bot. 40: 54, 1976.
O. resinifera (Bremer) Anderb. & Bremer, comb. nov. Basionym: *Relhania resinifera* Bremer, Opera Bot. 40: 48, 1976.
O. sedifolia (DC.) Anderb. & Bremer, comb. nov.

- Basionym: *Eclopes sedifolia* DC., Prodr. 6: 288, 1838 (= *Relhania sedifolia* (DC.) Harv.).
O. silicicola (Bremer) Anderb. & Bremer, comb. nov. Basionym: *Relhania silicicola* Bremer, Opera Bot. 40: 56, 1976.
O. squarrosa (L.) Anderb. & Bremer, comb. nov. Basionym: *Santolina squarrosa* L., Cent. 2. Plant. 30, 1756 (= *Relhania squarrosa* (L.) L'Hér.).
O. steyniae (L. Bolus) Anderb. & Bremer, comb. nov. Basionym: *Relhania steyniae* L. Bolus, Ann. Bolus Herb. 1: 191, 1915.
O. uniflora (L. f.) Anderb. & Bremer, comb. nov. Basionym: *Athanasia uniflora* L. f., Suppl. Pl. 362, 1781 (= *Relhania uniflora* (L. f.) Druce).
O. viscosa (L'Hér.) Anderb. & Bremer, comb. nov. Basionym: *Relhania viscosa* L'Hér., Sert. Angl. 1: 23, 1789.

References: Harvey, 1865; Smith, 1927; Mansfield, 1935; Bremer, 1976a (spp. 8–12, 14–20), Anderberg & Källersjö, 1988.

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