

THE CURRENT STATUS OF *CHAMAEMELES* (ROSACEAE: MALOIDEAE), A MADEIRAN ENDEMIC

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With 3 figures and 2 tables

ABSTRACT. The monotypic genus *Chamaemeles* is one of perhaps three genera endemic to Madeira. In this paper, results are presented from field trips made in January 1990 and October 1993 to study *Chamaemeles*. A total of 6 populations were observed. The local common name, Buxo da Rocha, or Box-of-the-Rocks, is most appropriate, for the shining evergreen leaves are reminiscent of a boxwood and the plants occur mostly near the tops of cliffs overlooking the ocean or on nearly vertical walls of ravines along rivers that flow into the ocean; the altitude is usually 100-400 meters. Populations seem to consist of 2-12 plants, but this is often not possible to ascertain because of the nearly inaccessible location of the plants. Most populations are on the southern part of the island, from west of Calheta to east of Funchal; a population is also known from the north side near Santana. A few plants occur on the neighboring islands of Porto Santo and Deserta Grande. The flowers have 10-15 stamens and only one carpel that is half or more adnate to the hypanthium and has two collateral ovules. The white fruits have short, somewhat fleshy, incurved calyx lobes, have abundant sclereids scattered throughout the flesh, contain a very hard, thick-walled stone, and the hypanthium becomes nearly fully adnate to the ovary. The embryo has complex folded and twisted cotyledons, unlike other Maloideae. Isozymes were used to obtain initial data on genetic diversity. Eleven enzyme systems were examined for 6 populations. Five of 23 loci were polymorphic, with a total of 11 alleles at the polymorphic loci. Several enzyme systems show strong evidence for duplicate levels of gene expression, which indicates that *C. coriacea* is polyploid (tetraploid).

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INTRODUCTION

While more than 200 species of flowering plants are endemic to Madeira and adjacent islands (HUMPHRIES 1979), *Chamaemeles* is one of perhaps only three endemic genera; the others are *Musschia* (Campanulaceae), which has two species, and *Monizia* (Apiaceae), which is monotypic and also occurs in the Salvage Islands. *Chamaemeles* has only one species, *C. coriacea*, and belongs to Rosaceae subfamily Maloideae.

For a number of years the senior author, in collaboration with J. B. PHIPPS of the University of Western Ontario, Canada, has been studying generic limits and evolution in Rosaceae subfamily Maloideae. A checklist of the species of Maloideae was completed early on in our studies (PHIPPS et al., 1990), a synopsis of genera was prepared (ROBERTSON et al., 1991), and a paper was prepared giving our views on the origin and evolution of the subfamily (PHIPPS et al., 1991). In addition, papers have been prepared summarizing the leaves (ROBERTSON et al., 1992), flowers (ROHRER et al., 1994), and fruits (ROHRER et al., 1992) of Maloideae. These papers were based primarily on observations of our own collections of living and/or alcohol preserved material. Much of this material was obtained from the living collections of botanical gardens and arboreta in the United Kingdom. Very few herbarium specimens of *Chamaemeles coriacea* were in herbaria, most of these were collected in the 1800s, and the current abundance of *C. coriacea* on Madeira was not known. In order to obtain material of *C. coriacea* for our studies of Maloideae, and to ascertain the current status of this species, two field trips to Madeira were undertaken by the senior author, the first in January 1990 and the second in October 1993. In addition to field work, herbarium specimens were examined at Herbario do Jardim Botânico da Madeira (MADJ), Museu Municipal do Funchal (MADM), and Museu de História Natural do Seminário do Funchal (MADS, housed at MADJ).

Taxonomic History

The genus *Chamaemeles*, and its sole species, *C. coriacea*, was first described by J. LINDLEY (1822), based on a specimen collected by F. MASSON in 1778 and sent to Sir JOSEPH BANKS. An illustration in this publication contained drawings of a flowering branch, a whole flower, and a longitudinal section of the central part of a flower showing the unilocular ovary with 2 ovules. LINDLEY put *Chamaemeles* in the family Pomaceae, which is now included in the Rosaceae as subfamily Maloideae (ROBERTSON et al. 1991).

LOWE (1833) published a much more complete account of *Chamaemeles coriacea*, based on his personal observations of living plants in Madeira. He included the first description of the pome-like fruit containing a single hard pyrene (endocarp) and the complex embryo.

In this publication, LOWE said that "*C. coriacea* is one of the rarest plants in Madeira; and at present I am only acquainted with one locality for it. This is on the sea-cliffs to the eastward of Funchal, about a mile out of the town along the Caniço road." By the time his *Manual Flora of Madeira* was published, LOWE (1868) was aware of at least four populations of *C. coriacea*: "Sea-cliffs and perpendicular sides of ravines on the S. coast, almost exclusively in the neighbourhood of Funchal, and never above a mile or two from the sea." By far the most comprehensive morphological description of the species is in LOWE'S *Flora*.

DECAISNE (1874) in his thorough monograph of Maloideae (as Pomacées) included a detailed description in Latin of *Chamaemeles*, and for the first time the convolute embryos were illustrated. In the last major monograph of Maloideae, KOEHNE (1890, 1891) divided the subfamily into two tribes, Crataegeae and Sorbeae, the former with fruits containing pyrenes and the latter with fruits having a cartilaginous core. *Chamaemeles* was included in the Crataegeae, placed just after *Cotoneaster* and *Pyracantha* and just before *Crataegus*.

Subsequent treatments of the plants of Madeira have only briefly mentioned or described *Chamaemeles coriacea*, without adding much new information (MENEZES 1914; HANSEN 1969). A color photograph of *C. coriacea* is included in Franquinho and da Costa (1992). *Chamaemeles* is not mentioned by SJÖGREN (1972), OBERDORFER (1975), or SYNGE and SYNGE (1979).

Distribution and Habitat

Chamaemeles coriacea grows on ledges near the tops of essentially vertical, basaltic cliffs facing the sea (Fig. 1A-C). It also occurs near the tops of steep walls of ravines above rivers up to 1-2 kilometers from the sea. Because it occurs on nearly vertical faces, access is very difficult. This species occurs today in at least 10 sites (Fig. 2), mostly along the south coast of Madeira from between Fajã da Ovelha to Paúl do Mar to near Caniço; also on the northeast side of Madeira at Rocha do Navio near Santana; Pico da Juliana, Porto Santo; and on Deserta Grande on a cliff above the islet of Doca. Brief descriptions of the populations visited in 1990 and 1993 are given below, and herbarium vouchers are at the Illinois Natural History Survey (ILLS) and the Museu Municipal do Funchal (MADM). Few plants were seen at each site, usually between 2 and 12.

1. On the west side of the ravine at Ribeira Brava, overlooking the town, west side of ravine, road to Apresentação, altitude 115 m. There are 3 or more plants on very steep slopes just below the road. Plants were in flower on 17 January 1990 and on 9 October 1993. Occurring with *Euphorbia piscatoria*, *Maytenus umbellata*, *Opuntia tuna*, and *Pelargonium inquinans*.

2. Just below the Levada dos Piornais São Martinho, west of Funchal, near where the new autoroute bridge is located, east side of ravine, altitude 150 m. There are at least 6 plants on steep slopes about 10 m below the levada. At this location, a small sucker shoot was observed coming off what appeared to be a rhizome of a much larger plant. Plants had mature fruit on 17 January 1990 and old flowers on 12 October 1993. Occurring with *Myrica faya*, *Olea europaea* subsp. *maderensis*, *Maytenus umbellata*, and *Globularia salicina*.

3. Above Fajã dos Padres, Quinta Grande, cliffs overlooking the ocean, altitude 320 m. (Fig. 1D). There are a few plants growing on ledges just below the top of the cliff. Plants had old flowers and young fruits on 16 January 1990 and were vegetative on 12 October 1993. Occurring with *Echium nervosum*, *Euphorbia piscatoria*, *Ficus carica*, *Globularia salicina*, and *Opuntia tuna*.

4. Lomba da Estrela, northwest of Calheta, west facing slope of ravine above Ribeira de São Bartholomeu, altitude 270 m. At least 4 large plants grow below the road on the very steep slopes of the ravine. In flower on 21 January 1990; plants observed only from a distance in 1993. Occurring with *Euphorbia piscatoria*.

5. Lazareto, Est. Nova da Igreja, between Funchal and São Gonçalo, ledges just below the top of a cliff overlooking the ocean, altitude 150 m. (Fig. 1A-C). Probably over 12 plants grow here over a lateral distance of 100 m. In flower on 23 January 1990, vegetative on 3 October 1993. João Sá Pereira Silva of the Museu Municipal do Funchal observed many flowers at this site in 1992, but very few flowers set fruit. Occurring with *Aloe arborescens*, *Olea europaea* subsp. *maderensis* and *Opuntia tuna*.

6. Quinta do Bom Sucesso, Jardim Botânico da Madeira, Funchal, east side of ravine above Ribeira João Gomes. Several plants grow spontaneously just below the top of very steep slopes of the ravine. In flower on 23 January 1990, vegetative on 11 October 1993. Occurring with *Myrica faya*.

In addition to the above populations that the senior author personally observed, the following locations for *Chamaemeles coriacea* have been vouchered recently by herbarium specimens.

7. Rocha do Navio, near Santana. This is the only record of the species from the north part of Madeira; it was collected by NÓBREGA in 1988 (MADJ).

8. Along the road between Fajã da Ovelha and Paúl do Mar, altitude 300-400 m., collected by C. SIMON in 1986 (2 specimens at MADM); young fruit on 23 March 1986, old fruit and many young flowers on 13 October 1989.

9. Deserta Grande, above the islet of Doca, altitude 200 m., on plant on a cliff. A fresh sample was collected in flower on 20 January 1990 and brought in to the senior author

when he was in Funchal; 2 plants were seen. Previously collected by NÓBREGA on 13 April 1983 (3 sheets at MADM), who noted it grew with *Sideroxylon marmulano*.

10. Porto Santo, Pico da Juliana. Collected by NÓBREGA 6 April 1953 (MADS).

In addition to the above, there are historical records from São Gonçalo and from Calheta, but it is not known if plants of *C. coriacea* are still extant at those locations.

In all cases, the plants of *Chamaemeles coriacea* grow just below the tops of cliffs or sides of ravines, and they are extremely difficult to reach or even observe. It may well be that there are numerous other populations that are unknown simply because they are not accessible. It is somewhat difficult to recognize *C. coriacea* from a distance, as its habit resembles several associate species (*Myrica faya*, *Olea europaea* subsp. *maderensis*, and *Maytenus umbellata*), although these species can be distinguished with field experience. Father Nóbrega hypothesized to the senior author in 1990 that Lowe may not have observed many populations of *C. coriacea* because its habitat would have been hidden by vegetation that grew above the cliffs in the 1800s.

According to LOWE (1833, 1868), *Chamaemeles coriacea* flowers from December to March, mostly December and January, depending on the earliness of the autumnal rains. Based on our limited observations in the field and on herbarium records, flowering can occur in June and October. According to Lowe, it takes nearly a full year for the fruits to mature, mostly in November or December; we have seen mature fruit in the field or on herbarium specimens from January, March, July, and October.

The common name, Buxo da Rocha, or Box-of-the-Rocks, is most appropriate, for the shining evergreen leaves are reminiscent of boxwood (*Buxus*) and the plants occur on the basaltic rock faces and ledges of cliffs and ravine walls. This same common name is applied to *Maytenus umbellata* (Celastraceae), which occurs in the same habitat, but is much more widespread on Madeira. LOWE (1833) related how Buxo da Rocha is not used by the ordinary residents of Madeira, who use "Buxo" for the common cultivated Box, *Buxus sempervirens*.

Nature of Endemism

There are basically two types of endemic species: neoendemics and paleoendemics. The former have arisen in their geographic regions of endemism from extant, evolutionary close, non-endemic relatives largely through the processes of adaptive radiation and vicarian evolution (schizoendemism of BRAMWELL, 1966) or polyploidy (apoendemism of Bramwell, 1966). Paleoendemism are relicts of formerly more widespread taxa that have become

extinct elsewhere, and they generally have these characteristics (DANIEL F. NICKRENT, Southern Illinois University, personal communication): 1) woody habit, 2) represent monotypic genera or families, 3) are sole living representatives of their lineage, 4) represent ancient divergence from their ancestors, and 5) may be reproductively compromised as a result of inbreeding depression.

Two genera endemic to Madeira are clearly neoendemics. *Musschia* and *Monizia* are segregates of more widespread genera, *Campanula* and *Melanoselenium*, respectively, and *Melanoselenium* is itself a segregate of *Thapsia*. HUMPHRIES (1979) did not recognize either *Musschia* or *Monizia*. On the other hand, *Chamaemeles* is a paleoendemic as defined by the above criteria. It is a woody shrub with no obvious close relatives within the Rosaceae subfamily Maloideae and appears isolated in the cladogram of PHIPPS et al. (1991). In this cladogram *Chamaemeles* is on the same clade as the monotypic *Dichotomanthes* of China; this clade is undoubtedly polyphyletic as these two genera have very little in common but both are very different from other Maloideae. Studies of reproductive biology are lacking for *Chamaemeles*, but the lack of extensive production of fruit may be indicative of inbreeding depression (or other factors).

SUNDING (1979) does not mention *Chamaemeles* in his discussion of Macaronesian endemics, but he does consider a greater part of the Macaronesian endemic element to be a relict flora of a much wider distribution, especially a humid subtropical flora that occurred in Europe and North Africa until the Late Tertiary. *Chamaemeles coriacea* certainly fits this pattern. There are many non-endemic relict species and some neoendemic species in the Clethro-Laurion forest of SJÖGREN (1972) that takes its name from the dominant tree species, *Clethra arborea* and several genera of Lauraceae (*Apollonias*, *Laurus*, *Ocotea*, *Persea*). This forest is still prevalent in the higher elevations of the central part of Madeira. There appear to be fewer relict, paleoendemic species in the lower elevation Aeonio-Lytanthion association of SJÖGREN (1972) where *Chamaemeles* occurs, although many neoendemic species appear in this association.

Morphology

Chamaemeles coriacea is a large multi-stemmed, evergreen, unarmed shrub. It is difficult to ascertain the height of plants since they grow below the tops of cliffs and on ledges of ravines. However, the plants are considerably larger than previously published heights of 3-5 feet (LOWE 1868) and 1-1,5 m (FRANQUINHO and DA COSTA 1992). Our estimates are at least 3 m tall for most plants seen in this study (see Fig. 1D). The crown is broad and the plants are nearly as wide as tall. Plants occurring on cliffs facing the ocean are often more or less symmetrical and nearly globose, although the side of the plant facing the ocean can have a flatish oblique plane evidently caused by wind. Plants in ravines can be

quite straggly when growing in competition with other species. Both long terminal shoots and short lateral spurs are present on the branches, and they are straight, stiff, and rather stout (Fig. 1D). First year branches have scattered fine white trichomes, and the long shoots are reddish in color when elongating. The bark is gray and smooth when young, with horizontal lenticels, developing thin vertical wrinkles and peeling on older stems, and mature bark on older plants has thin plates and narrow, shallow, irregular, vertical fissures. The inner bark is orangish.

The leaves (Fig. 1D) are simple, coriaceous, evergreen, and dark glossy green above with a thick translucent epidermis, paler below. The leaves are glabrous or with a few fine white hairs below on the midrib; the venation is camptodromous. On long shoots, the leaves alternate along the twigs, while on spur shoots the leaves are clustered at the tips. Leaf size is variable, generally varying between 20-50 mm long and 8-18 mm wide. The overall shape is usually spatulate and distinctly wider above the middle. The apices are acute to rounded and often slightly retuse with a small mucro. The margins are remotely and faintly crenate with a few widely spaced rounded teeth, each terminated by a small gland. The bases taper very gradually to a short petiole. The stipules are tiny, triangular, and deciduous.

The inflorescences are small panicles or racemes produced at the tips of new growth of the year and from lateral spurs on 1- and 2-year old branches; they are often produced in great abundance. Small leaves occur at the bases of inflorescences, and the bracts are small, reddish, and deciduous.

The flowers (Fig. 3A) are perfect and rather small, about 6-7 mm in diameter, and are among the smallest flowers in subfamily Maloideae (ROHRER et al. 1994). LOWE (1868) noted that the flowers have a strong disagreeable odor like that of *Berberis vulgaris*. The hypanthium is well developed and lined with nectar producing tissue. The 5 calyx lobes are erect, triangular, and only about 0.5-0.9 mm long; they are glabrous except for a tuft of apical hairs. The 5 petals are white, with a small bright pinkish abaxial stripe in bud. Each petal has a distinct claw and a roundish, erose, cupped blade. In open flowers, the petals are held horizontally. The stamens number 10-15. In bud, the filaments fold inwards in half, becoming erect at anthesis and about equaling the petals in length; the anthers are yellow. The carpel is solitary and about half-adnate to the hypanthium (Fig. 3A), with the ovary then half-inferior; there are several tufts of hairs at the base of the superior part of the ovary. The style is slightly shorter than the filaments and is terminated by an oval stigma. There is one locule that contains two collateral, erect ovules.

The fruit (Fig. 3B) is a whitish or pale cream-colored pome. It is smooth, rather

glossy, 7-12 mm in diameter, and more or less globose to pyriform with a flat-top. The flesh is homogeneous with abundant sclereids scattered throughout. In fruit, the ovary is nearly fully adnate to the hypanthium, and free from the pyrene only at the very top. The calyx lobes are persistent, becoming slightly fleshy and incurving to enclose the persistent stamens. There is one very hard, thick-walled (ca. 1 mm) pyrene per fruit; it can be up to 7 mm long and 5 mm wide. The pyrene (Fig 3C, D) is smooth; near the apex is a circumscissile ring that demarcates the free and adnate parts of the ovary and hypanthium. This top free part of the pyrene is narrower and protrudes into the small cavity formed by the free part of the hypanthium. The embryo is quite elaborate (Fig. 3E-H). The two cotyledons are folded longitudinally and then complexly interfolded and twisted. LOWE (1868) describes the cotyledons as "beautifully convolute, appearing in a transverse section like 2 leaves or laminae rolled together spirally." Even this vivid description does not fully describe the labyrinth formed by the cotyledons.

Within subfamily Maloideae, *Chamaemeles* is quite distinct. Only a few species of *Crataegus*, *Cotoneaster*, and the monotypic *Dichotomanthes* have a single carpel. In phenetic analysis of the fruits, *Chamaemeles* clusters with *Cotoneaster* and *Pyracantha* because of the incurved, slightly fleshy calyx lobes and the presence of a pyrene (ROHRER et al. 1992). The embryo with folded and convolute cotyledons is unlike that of any other Maloideae and other Rosaceae for that matter. The only other Rosaceae with a convolute embryo is the monotypic *Oemleria* (*Osmaronia*) of northwestern North America, which belongs to subfamily Amygdaloideae (Prunoideae). Subfamily Maloideae is often thought to be of allopolyploid origin between subfamily Amygdaloideae and subfamily Spiraeoideae (see discussion in ROBERTSON 1974 and PHIPPS, ROBERTSON, ROHRER and SMITH 1991).

Genetic Diversity

To obtain initial data on genetic diversity within *Chamaemeles coriacea*, 11 enzyme systems were examined for 6 different populations (Quinta Grande, Levada dos Piornais S. Martinho, Ribeira Brava, Lombo da Estrela, Lazareto, and Jardim Botânico da Madeira). Methodologies followed those described in DICKSON et al. (1991). The results are shown in Table 1. Our data were insufficient to generate complete genetic diversity statistics because we did not perform genetic investigations on the polymorphisms observed and we had a limited sample size. For *C. coriacea* there were 5 polymorphic loci out of 23 (proportion ratio of 0.22) isozyme loci. In comparison, 9 of 17 (0.53) isozyme loci were polymorphic in *Malus fusca* and 6 of 17 (0.35) in *M. angustifolia* (DICKSON et al. 1991), two widespread species of subfamily Maloideae in North America. Thus, this measure of genetic diversity is lower in the island endemic than in either of the widespread species. However, the proportion ratio of 0.22 for *Chamaemeles coriacea* does reflect a reasonable level of polymorphism.

Genetic diversity as measured by isozymes has been summarized by HAMRICK and GODT (1990) and discussed in the context of endemics in CRAWFORD et al. (1992). According to the latter authors, endemics have a lower proportion of polymorphic loci than non-endemic species, with a mean of 0.50 for all plant species studied vs. a mean of 0.46 for all endemic species. Island endemics have an even lower proportion of polymorphic loci, and in the data presented by DEJOOE and WENDEL (1992) the mean proportion of polymorphic loci for 64 island endemic taxa is 0.25. This mean is slightly greater than the figure of 0.22 for *Chamaemeles coriacea*. An extreme example of low genetic diversity of an island endemic is *Lactoris fernandeziana* (Lactoridaceae) of the Juan Fernandez Islands, where a study of 22 presumptive loci resolved from 10 enzymes showed no variation in the plants examined (CRAWFORD et al. 1994).

There are a total of 29 alleles across 23 loci (1.26 alleles/locus) in *Chamaemeles coriacea*. Another comparison that can be made is the number of alleles per polymorphic locus. *C. coriacea* had 11 alleles at 5 loci (2.2 alleles/locus). In comparison, *Malus fusca* had 21 alleles at 9 loci (2.3 alleles/locus) and *M. angustifolia* had 16 alleles at 6 loci (2.7 alleles/locus). Thus, while only a few loci in *C. coriacea* were polymorphic, this still represents a significant level of genetic diversity.

The number of duplicate isozyme loci for *Chamaemeles* and three other genera of subfamily Maloideae are presented in Table 2. Genetic data are not available for all systems, and in certain cases the isozyme phenotype is probably incomplete; as a result the phenotype is conservatively interpreted regarding gene number. Asterisks indicate systems in which there is strong evidence for duplicate (i.e. tetraploid) level of gene expression. As mentioned above, subfamily Maloideae is considered to be of allopolyploid origin. While a chromosome count for *C. coriacea* is lacking, isozyme data does provide supporting evidence that this species is polyploid.

ACKNOWLEDGMENTS

We thank MANUEL JOSÉ BISCOITO of the Museu Municipal do Funchal for much assistance in planning the field trips, providing facilities and transportation, and making the visits to Madeira so productive and enjoyable. We also thank SUSANA S. FONTINHA and JOSÉ AUGUSTO, Jardim Botânico da Madeira. REV. M. DE NÓBREGA provided information on extant locations and accompanied the senior author in the field. JOÃO SÁ PEREIRA SILVA, GRAHAM QUINN, and ALAIN OBRIOT also helped with field work. Valuable reviews of the manuscript were made by DANIEL F. NICKRENT and GEOFFREY A. LEVIN; S. C. MCKAY made editorial comments. Financial assistance was provided by the Research Board of the University of Illinois.

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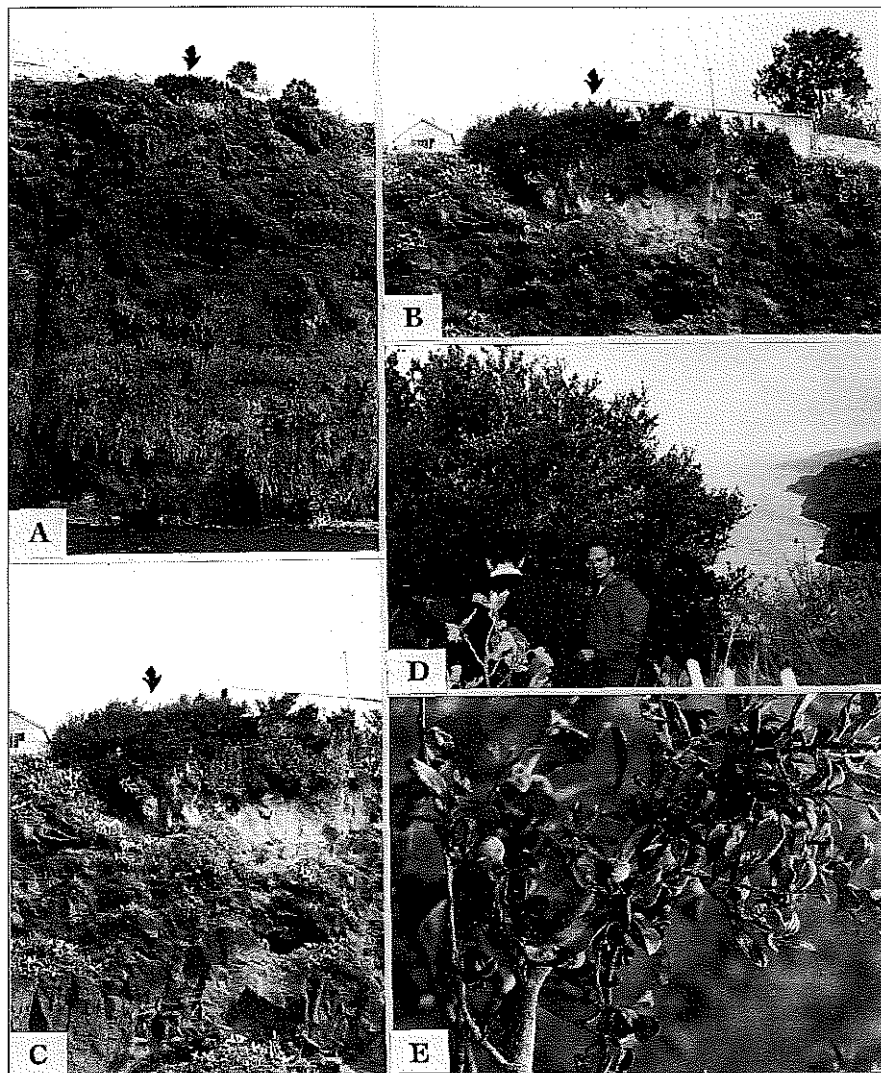


Figure 1 - Habitat and habit of *Chamaemeles coriacea*. A - View of cliff at Lazareto, east of Funchal, from the sea with plants of *C. coriacea* (marked with arrow) growing just below top of cliff. B, C - Same view, but with telephoto lens. D - Plant of *C. coriacea* growing just below Quinta Grande (photo by GRAHAM QUINN). E - Close-up of branches with leaves and mature fruit.

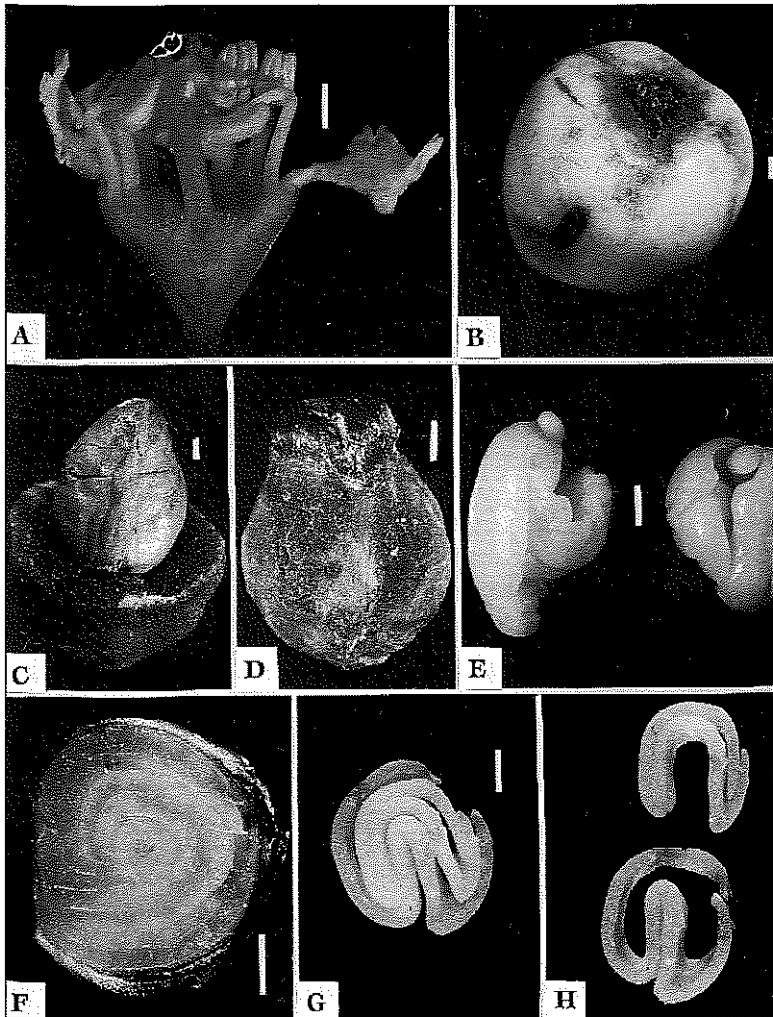


Figure 3 - Flower, fruit, pyrene, and embryo of *Chamaemeles coriacea*; white scale bar to right of each photograph represents 1 mm. A - Flower, not quite fully open, in longitudinal section, note that the upper part of the ovary is free from the hypanthium. B - Whole fruit, note persistent and incurved calyx lobes. C - Fruit with half of flesh removed to show pit (the diagonal line is an artifact of cutting). D - Whole pyrene, note the constricted upper part that is free from the hypanthium and protrudes into the opening. E - Two views of whole embryos. F - Embryo in cross section near top, surrounded by seed coat. G - Embryo in cross section, near bottom. H - The two cotyledons from "G" lifted apart to show folding.

TABLE 1 - Summary of allozyme polymorphism in *Chamaemeles coriacea*.

System	No. of Loci	Polymorphic loc	No. of Alleles
AAT	2	0	2
DIA	2	1	3
GDH	2	0	2
GPI	3*	0	3
MDH	2	1	4
PGD	2	1	3
PGM	3*	2	5
PRX	2	0	2
SKDH	1	0	1
SOD	1	0	1
TPI	3*	0	3
Totals	23	5	29

* = more loci than expected in a diploid plant.

AAT = aspartate aminotransferase; DIA = NADH diaphorase; GDH = glutamate dehydrogenase; GPI = Glucosephosphate isomerase; MDH = malate dehydrogenase; PGD = 6-phosphogluconate dehydrogenase; PGM = phosphoglucomutase; PRX = peroxidase; SKDH = shikimate dehydrogenase; SOD = superoxide dismutase; TPI = Triosephosphate dehydrogenase.

TABLE 2 - Number of Duplicate Isozyme Loci in 4 Maloid Genera.

System	<i>Chamaemeles</i>	<i>Cotoneaster</i> ⁽⁴⁾	<i>Pyracantha</i> ⁽⁴⁾	<i>Malus</i> ⁽⁵⁾
AAT	2	2	2	4*
GPI	3*	3*	3*	3*
MDH	3*	4*	4*	3*
PGD	2	2	not available	3*
PGM	4*	2	2	5*
TPI	3*	3*	3*	3*

* = more loci than expected in a diploid plant.

4 From Phipps, Weeden and Dickson 1991 and Weeden and Phipps, unpublished data.

5 From Weeden 1986.