THE ORCHIDS

Although the orchid floras of Tonga, Niue, and the Cook Islands are not rich, they are diverse. Altogether, 52 species in 28 genera are included in this field guide. Given the sporadic occurrence of orchids and their favored habitats as forest floor terrestrials or canopy epiphytes, we anticipate that more species will be added to the flora in the future. If you find something that does not key out in this guide, the authors would be very interested to hear from you. You may well have found a novelty.

Previous Treatments. Yuncker (1959) provided a list of the orchids of Tonga that included 20 species in 15 genera. Yuncker (1943) and Sykes (1970) have provided records of Niue orchids, the former listing 13 species in 10 genera, the latter 18 species in 16 genera. Both included the introduced *Vanilla planifolia* (as *V. fragrans* and *V. mexicana*, respectively). Hallé *et al.* (1998) listed six species in five genera for Rarotonga. In the present account, 43 species in 25 genera are recognized for Tonga, 11 genera being new to the archipelago (since Yuncker 1959). Seventeen native species in 15 genera are reported from Niue, and 13 species in 11 genera from the Cook Islands. In an orchid flora of the Austral Islands, which are a southeastern extension of the Cook Islands, Hallé (1980) listed 11 native species, 8 of which are treated in the present publication. The introduced vanilla orchid (*Vanilla planifolia*) is reported from all four island groups. A total of 51 native species in 27 genera are included in this book, plus the introduced vanilla orchid.

Affinities and Origin of the Orchids. The orchids of our region have strong affinities with those of the neighboring archipelagos, which, in turn, have close affinities with the orchids of the Malay Archipelago, especially New Guinea. Most of the orchids of our region are found elsewhere in the Pacific, mostly in adjacent archipelagos such as Samoa, Fiji, or New Caledonia. Others are yet more widespread: *Calanthe triplicata* has a distribution that extends from Madagascar through S.E. Asia and the Malay Archipelago to N.E. Australia and the S.W. Pacific islands; *Corymborkis veratrifolia*, *Eulophia spectabilis*, and *Geodorum densiflorum* are found from the Asian mainland and the Malay Archipelago to N.E. Australia and the S.W. Pacific islands; and *Taeniophyllum fasciola*, a minute epiphytic orchid, is found throughout the tropical Pacific as far east as Pitcairn Island. Only one species in Tonga (*Robiquetia tongaensis*) and one in the Cook Islands (*Habenaria amplifolia*) are endemic to their respective islands. Niue has no endemic species.

Why are the species of the Pacific islands so widespread? The answer lies in their peculiar biology. All orchids have small, light seeds devoid of any endosperm, and comprise an embryo of just over 100 cells covered by a seed coat that is more or less waterproof. The seed pods of orchids can contain hundreds or even thousands of seeds. In windy places favored by orchids, the light ripe seeds can be blown long distances from the mother plant. When they arrive at a new locality, the seed can germinate if it meets the right fungus, one that has *mycorrhizal* properties. Such fungi have *hyphae* (fungal threads) that enter the orchid embryo, but the orchid cells can extract nutrients from the fungus as the embryo begins to germinate and grow. A body called a *protocorm* is produced when the embryo successfully germinates. Roots, a shoot, and leaves are produced from this so that eventually the orchid can photosynthesize and grow into a mature plant. Many orchids use common fungi to germinate and they, having light spores, are also widespread. Thus, orchid seeds reaching remote islands, even volcanic ones, have a chance of growing and flowering. It is no coincidence that many island orchids are self-pollinating and can produce seed without the presence of their natural pollinating insect. This is true of the orchids of our region.

WHAT IS AN ORCHID?

The orchids found in Tonga, Niue, and the Cook Islands are a diverse group. The smallest one to be found there is the tiny *Taeniophyllum fasciola*, which is scarcely 2 or 3 cm in height with flowers 1–2 mm across, whereas the terrestrial *Corymborkis veratrifolia* may reach a meter or more in height, with flowers several cm long. *Taeniophyllum* and *Didymoplexis micradenia* have no leaves, but most other orchids have green leaves of various shapes and sizes. Some orchids (referred to as terrestrial) live on the ground while others grow perched on trees (epiphytes) or rocks (lithophytes). The introduced vanilla is a liana that can climb many meters up forest trees, using its roots for support. What then unites these diverse plants into the family called the Orchidaceae? The distinctive features of orchids that separate them from other flowering plants lie primarily in their flowers.

The plant. The vegetative features of orchids are, if anything, more variable than their floral ones. This is scarcely surprising when the variety of habitats in which orchids are found is considered. Tropical orchids grow in almost every situation: on the permanently moist floor of the lowland tropical rain forest; on the uppermost branches of tall forest trees where heavy rainfall is followed by scorching sun for hours on end; on rocks; and in grassy areas found on landslips and roadsides. The major adaptations seen in orchid vegetative morphology allow them to withstand adverse environmental conditions, particularly the problems of water conservation on a daily and seasonal basis.

That tropical orchids might suffer from periodic water deficits is not immediately obvious. However, rainfall is not continuous; even the wettest habitats and the rainfall patterns are markedly seasonal in many places in the tropics. Furthermore, most tropical orchids are epiphytic, growing on the trunks, branches, and twigs of trees, or as lithophytes on rocks. In these situations, water run-off is rapid and the orchids can dry quickly in the sunshine that follows the rain. Many orchids have marked adaptations of one or more organs that allow them to survive these periodic droughts. Some of these adaptations are as dramatic as those encountered in the cactus family Cactaceae. The stem can develop into a water-storage organ. This is so common in tropical orchids that the resulting structure has been given a technical name, a ***pseudobulb***. Pseudobulbs comprise several internodes in the genus *Dendrobium*, while in *Bulbophyllum* they comprise one internode only. Pseudobulbs are also found in many terrestrial orchids and can grow either above the ground, as in *Calanthe*, or underground, as in *Geodorum*.

A few terrestrial orchids, such as *Habenaria* and *Peristylus*, lack pseudobulbs, but have underground ***tubers*** that enable the plant to survive drought. In suitable conditions the new growth occurs from one end of the tuber. In other orchids, such as *Zeuxine* and *Goodyera*, the stems are succulent but not swollen. The horizontal stem or ***rhizome*** creeps along the ground in the leaf litter, and erect shoots bearing the leaves are sent up periodically.

The leaf is another organ that has undergone dramatic modification in orchids. Fleshy or leathery leaves with restricted stomata, such as those of *Dendrobium* and *Bulbophyllum* species, are common. In *Taeniophyllum* the leaves have been reduced to scales, and photosynthesis takes place in the flattened green roots. Only one island orchid, *Didymoplexis micradenia*, is leafless and lacks chlorophyll altogether; it is termed ***saprophytic***. Lacking chlorophyll, it cannot photosynthesize its own food and must obtain all of its nutrition from the mycorrhizal fungus with which it is associated.

Orchid species with green leaves used for photosynthesis are termed ***autotrophic***. The terrestrial species usually have much thinner-textured leaves than their epiphytic cousins. In lowland forest, the perpetually moist atmosphere and lack of direct sunlight means that such leaves are not subject

to drought. Some of the terrestrial species of the forest floor have beautifully marked leaves. In *Goodyera*, *Zeuxine*, *Erythrodes*, and their relatives, the leaves can range from green to deep purple or black and may be mottled or reticulate-veined with silver.

The roots themselves are highly modified in most epiphytic orchids. They provide both attachment to the substrate and also absorb water and nutrients in a periodically dry environment. The roots have an actively growing tip; the older parts are covered by an envelope of dead empty cells called a *velamen*. The velamen protects the inner conductive tissue of the roots and may also aid in the uptake of moisture from the atmosphere, acting almost like blotting paper for the orchid.

Life in the tropics can be inhospitable even for orchids. In those regions with a more marked seasonality, conditions may be very inhospitable for orchids at certain times of the year. Even tropical forests can have periods of relative drought, during which the orchids have to survive days or even weeks without rain. In these conditions, tropical orchids without water-storage capabilities in their stems or leaves can drop their leaves and survive on the moisture stored in their roots that are protected by their cover of velamen.

The inflorescence. Orchids bear their flowers in a variety of ways. Even within the same genus, different species have different ways of presenting the flowers. Most orchids in the Pacific islands have inflorescences bearing two or more flowers, usually borne on a more or less elongate floral axis comprising a stalk called the ***peduncle*** and a portion bearing the flowers called the ***rachis***. In *Phaius tankervilleae*, the flowers are borne in an erect, elongate, unbranched ***raceme*** with the flowers arranged in a lax spiral around the rachis. Its individual flowers are attached to the floral axis by a stalk called the ***pedicel***. In some species, such as *Peristylus tradescantifolius*, pedicels are virtually absent and the flowers are sessile on the axis; such an inflorescence is termed a ***spike***.

Some interesting variations on the multi-flowered inflorescence occur in the genus *Bulbophyllum*. In several species, all the flowers are borne facing the same side of the rachis, this being called a ***secund*** inflorescence. The most spectacular group, however, comprises species in which the rachis is so contracted that the flowers all appear to come from the top of the flower stalk in an umbel, with the inflorescence somewhat resembling the head of a daisy. These bulbophyllums, such as *Bulbophyllum longifolium*, were for this reason formerly considered to be in the separate genus *Cirrhopetalum*. Compound inflorescences with many flowers are uncommon in island orchids, but those that are branched are termed ***panicles***. In many species the flowers are borne one-at-a-time either sessile or on a short or long peduncle. Solitary flowers can be found in many genera, such as *Bulbophyllum*.

The flower. Orchid flowers are simple in structure and yet highly modified from the more typical monocotyledon flower exemplified by a *Trillium* or *Lilium*, to which orchids are very distantly allied. Monocots characteristically have their floral parts arranged in threes or multiples of three, and orchids are no exception. This can most easily be seen in the two outer whorls of the flower. For example, the common Pacific island orchid *Phaius tankervilleae* is similar in general floral structure to the majority of orchids from these islands. Its floral parts are situated at the apex of the ***ovary*** that is tripartite in cross section. The outermost whorl of the flower, the calyx, consists of three ***sepals*** that are petal-like and colored yellow with a red stripe in the middle. The two lateral sepals differ slightly from the third, which is called the ***dorsal*** or ***median sepal***. In some orchids, such as dendrobiums and bulbophyllums, the ***lateral sepals*** form a more or less conical chin called a ***mentum*** at the base.

The corolla of *Phaius tankervilleae* comprises three ***petals*** that are brightly colored. The two lateral petals, resembling the dorsal sepal in coloration and shape, are uppermost in the flower and differ markedly from the third petal, which lies at the bottom of the flower. This third petal, called the ***lip*** (or ***labellum***), is highly modified, 3-lobed, and bears a short spur or nectary at the base. The spur can be longer or more saccate in other orchids and can contain callosities (ridges or keels) that are diagnostic for some species. The upper surface of the lip in some orchids may be adorned with a callus of raised ridges, lamellae, tufts, or areas of hairs or glands. The lip is an important adaptation of the orchid in facilitating cross pollination. It can be imagined as a brightly colored flag to attract potential and specific pollinators that are then guided towards the pollen and stigmatic surface by the form of the callus. The lip, therefore, can be supposed to act as a landing platform, and the callus structure as a guidance system for the pollinator.

The central part of the orchid flower shows the greatest modifications to the basic monocotyledon pattern. The major evolutionary forces at work in orchids have been the reduction in the number of floral parts and the fusion of the male and female organs into a single structure. The fused organ in the center of an orchid flower is called the ***column***. In *Phaius tankervilleae* and in most Pacific island orchids, a single *anther* lies at the apex of the column. The pollen in the anther is not powdery as in most plants, but is borne in eight discrete masses called ***pollinia*** (single, ***pollinium***). The pollinia are attached to a sticky mass called the ***viscidium*** (plural, ***viscidia***). In other species the number of pollinia may be two, four, or rarely six, and these are attached to the viscidium either directly or by a stalk called a ***stipe*** in most epiphytic orchids, and a ***caudicle*** in most terrestrial ones.

The ***stigma***, the receptive surface on which pollen alights and germinates, is also positioned on the column in the center of the orchid flower, on its ventral surface. The stigma is a sticky, lobed depression situated below and behind the anther in most orchids, but in some terrestrial genera, such as *Habenaria* and *Peristylus*, the stigma is bilobed with the receptive surfaces at the apex of each lobe. In many species the pollen masses are transferred to the stigmatic surface by a modified lobe of the stigma called the ***rostellum***. This is developed in *Phaius tankervilleae* as a projecting flap that catches the pollen masses as the pollinator passes beneath it on its way out of the flower.

An interesting feature of the development of most orchid flowers is the phenomenon of ***resupination***. In bud, the lip lies uppermost in the flower, while the column lies lowermost. In species with a pendent inflorescence, the lip will, therefore, naturally lie lowermost in the flower when it opens. However, this would not be the case in the many species with erect inflorescences, such as *Phaius tankervilleae*. Here the opening of the flower would naturally lead to the lip assuming a place at the top of the flower above the column. In most species this is not the case, and the lip is lowermost in the flower. This position is achieved by means of a twisting (resupination) of the flower stalk or ovary through 180º as the bud develops.

Conclusions. An understanding of the floral and vegetative structure of orchids provides the clues needed to identify orchids. Knowledge of their floral morphology is critical for naming orchids because they are, for the most part, classified into genera and species on the finer details of the structure of their sepals, petals, lip, and column. Floral dissections provide the essential information for identification. For most species the shape of the sepals, petals, and especially the lip provides all of the information the reader needs. However, for the more critical taxa, details of the column, anther, pollinia, and rostellum may be needed before accurate identification is possible. The vegetative features also provide orchid growers with an idea of what to give their orchids to obtain optimal conditions for growth. If the seasonal nature of the growth found in many orchids is ignored, they will rapidly perish.

ORCHIDACEAE

Herbs (or rarely scrambling vines), perennial, terrestrial, epiphytic, or lithophytic, autotrophic or rarely saprophytic, with rhizomes, tubers or rootstocks with mycorrhizal fungi in the roots. *Stems* either sympodial or less commonly monopodial, usually leafy, but leaves sometimes reduced to bract-like scales, one or more internodes at the base often swollen to form a "pseudobulb;" epiphytic species with aerial, assimilating adventitious roots, often bearing one or more layers of dead cells (velamen). *Leaves* 1–many, glabrous or very rarely hairy, entire in some cases except at the apex, alternate or occasionally opposite, often distichous, frequently fleshy or leathery, sometimes terete or canaliculate, almost always with a basal sheath that frequently sheathes the stem, sometimes articulated at the base of the lamina and sometimes with a false petiole. *Inflorescence* erect to pendent, spicate, racemose, or paniculate, one- to many-flowered, basal, lateral, or terminal, the flowers rarely secund, subumbellate, or distichously arranged. *Flowers* small to large, often quite showy, hermaphroditic (or rarely monoecious and polymorphic outside the region), sessile or variously pedicellate, most often twisted through 180°, occasionally not twisted or twisted through 360°. *Ovary* inferior, unilocular and the placentation parietal (or rarely trilocular and the placentation axile). *Sepals* usually free but sometimes variously adnate, the median (dorsal) one often dissimilar to the laterals, the laterals sometimes adnate to a column-foot to form a saccate, conical, or spur-like mentum. *Petals* free or rarely partly adnate to sepals, similar to sepals or not, often showy. *Lip* entire, variously lobed or two- or three-partite, ornamented or not with calli, ridges, hair cushions, or crests, with or without a basal spur or nectary, margins entire to laciniate. *Column* short to long, with or without a basal foot, occasionally winged or with lobes or arms at apex or ventrally; anther one (or rarely two or three outside region), terminal or ventral on column, cap-like or opening by longitudinal slits; pollinia mealy, waxy or horny, sectile or not, 2, 4, 6, or 8, sessile or attached by stalks to one or two sticky viscidia; stigma 3-lobed, the midlobe often modified to form a rostellum, the other lobes either sunken on the ventral surface of the column behind the anther or with two lobes porrect. *Fruit* a capsule, usually opening laterally by 3 or 6 slits; seeds numerous, dust-like, lacking endosperm, rarely winged.

The orchids comprise one of the largest families of flowering plants, with an estimated 800 genera and 25,000 species, with some estimates suggesting as many as 30,000 species. They are distributed in all continents except for Antarctica, but are most numerous in the humid tropics and subtropics. Altogether, 28 genera of orchids are reported from Tonga, Niue, and the Cook Islands. Some 43 native species are found in Tonga, 30 being terrestrial, the remainder epiphytic. One epiphytic Tongan species is endemic (*Robiquetia tongaensis*). Seventeen native species have been found on Niue, nine of them terrestrial and the rest epiphytic. Thirteen native species are reported from the Cook Islands, eight of them terrestrial and five epiphytic; only one of them is endemic (*Habenaria amplifolia*). The affinities of the orchids are with those of other S.W. Pacific islands and New Guinea. Orchids are extensively grown around the world as ornamentals, but other economic uses are few. Two species of *Vanilla* are grown commercially in the Pacific islands, especially in the Society Islands, to produce the flavoring vanilla. One, *Vanilla planifolia*, has been introduced to Niue and the Cook Islands, where it has escaped into the wild.

The classification of the family is currently the subject of some debate, particularly the number of subfamilies that should be recognized and the placement of certain tribes, subtribes, and genera. The classification of Chase *et al.* (2003), elaborated in Pridgeon *et al.* (1999, 2001, 2003, 2005), which is strongly supported by recent molecular, embryological, and morphological analyses, is followed here. They recognize five subfamilies: Apostasioideae, Cypripedioideae, Vanilloideae, Orchidoideae, and Epidendroideae. Only the last three subfamilies are found in our region: Vanilloideae (genus 1), Orchidoideae (genera 2–9), and Epidendroideae (genera 10–28).

In the species accounts, an exclamation mark after the herbarium designation letter indicates that the lead author has personally examined the specimen. A † after B (Berlin) indicates that the type was probably destroyed during World War II.

ARTIFICIAL KEY TO THE GENERA

1. Orchids liana-like or vine-like ..... 1. ***Vanilla***
1. Orchids not as above
  2. Stems leafless or apparently so at flowering time
    3. Plants terrestrial; roots brown, underground
      4. Leaves absent; stem buff-colored; plant saprophytic ..... 12. ***Didymoplexis***
      4. Leaves present before flowering, green, photosynthetic ..... 11. ***Nervilia***
    3. Plants epiphytic; roots greenish, photosynthetic, attached to tree bark or hanging freely ..... 24. ***Taeniophyllum***
  2. Stems not as above
    3. Plants terrestrial
      4. Plants with fleshy underground tubers or pseudobulbs either on or below the surface of the soil
        5. Leaves solitary, heart-shaped or ovate ..... 11. ***Nervilia***
        5. Leaves several, linear, lanceolate, or oblanceolate
          6. Inflorescence with apex recurved and facing towards ground ..... 28. ***Geodorum***
          6. Inflorescence erect
            7. Flowers small, arranged in a spiral; lip entire, porrect ..... 7. ***Spiranthes***
            7. Flowers not obviously spirally arranged; lip 3-lobed, pendent
              8. Plant with pseudobulbs; leaves 2–3, borne at base or towards pseudobulb apex; sepals and petals 7–9 mm long ..... 27. ***Eulophia***
              8. Plant with tubers; leaves 5–7, thin-textured, borne in middle or apical part of slender stem; sepals and petals variable
                9. Sepals and petals less than 5 mm long; spur less than 8 mm long ..... 8. ***Peristylus***
                9. Sepals and petals more than 10 mm long; spur more than 25 mm long 9. ..... 9. ***Habenaria***
      4. Plants with a fleshy or woody underground, non-tuberous rhizome
        5. Erect stems woody, growing from a woody rhizome; inflorescences lateral and terminal; flowers more than 2 cm long; bracts not noticeably distichous ..... 10. ***Corymborkis***
        5. Erect stems fleshy, growing from a fleshy creeping rhizome or pseudobulbous from a creeping rhizome; inflorescences terminal; flowers less than 1 cm long; bracts noticeably distichous
          6. Stems similar to creeping rhizome, fleshy but not swollen
            7. Lip uppermost in flower ..... 4. ***Hetaeria***
            7. Lip lowermost in flower
              8. Flower lip with a spur
                9. Leaves dark green with a longitudinal white stripe; spur conical, entire or slightly bilobed at tip, with stalked two glands within ..... 5. ***Vrydagzynea***
                9. Leaves green; spur cylindrical, bilobed at tip, with 2−4 sessile glands within ..... 2. ***Erythrodes***
              8. Flower lip lacking a spur but often with a saccate base
                9. Lip with papillae or glands in saccate basal part ..... 3. ***Goodyera***
                9. Lip lacking glands within basal part ..... 6. ***Zeuxine***
          6. Stems dissimilar from rhizome, often swollen and pseudobulbous
            7. Inflorescences lateral, from base or sides of the pseudobulb or stem
              8. Flowers urn-shaped ..... 16. ***Acanthephippium***
              8. Flowers not urn-shaped

9. Tepals pink or rose-purple, rarely white, never turning blue when bruised; lip lacking a spur; callus prominently bilobed between the narrowly oblong, erect side lobes ..... 15. ***Spathoglottis***
9. Tepals white, yellow or brown with a purple lip, turning blue when bruised; lip with a spur; callus not as described above
10. Column short, almost as broad as long, adnate to the base of the lip; lip deeply 3- or 4-lobed, more or less flat, with a basal callus ..... 13. ***Calanthe***
10. Column elongate, more or less free from lip; lip obscurely lobed, more or less tubular, lacking a basal callus ..... 14. ***Phaius***

7. Inflorescences terminal
8. Lip more or less as broad as long; erect, uppermost in the flower; column very short, not extending beyond the base of the lip ..... 18. ***Crepidium***
8. Lip broader than long, recurved or porrect, lowermost in flower; column elongate, incurved, at least half length of the lip ..... 17. ***Liparis***

3. Plants epiphytic or rarely lithophytic
4. Plants with bilaterally compressed, iridiform leaves; flowers less than 3 mm across, in dense cylindrical spike ..... 19. ***Oberonia***
4. Plants with dorsiventrally flattened or terete leaves; flowers larger, in lax to dense spikes or solitary
5. Plants sympodial, each growth determinate; inflorescences terminal and lateral
6. Pollinia 4
7. Inflorescence lateral ..... 23. ***Bulbophyllum***
7. Inflorescence terminal or axillary from upper nodes ..... 22. ***Dendrobium***
6. Pollinia 6 or 8
7. Stems elongate with well-spaced distichous leaves; inflorescences lateral; pollinia 6 ..... 20. ***Appendicula***
7. Stems short with leaves borne more or less in a fan-shape; inflorescences borne amongst leaves; pollinia 8 ..... 21. ***Phreatia***

5. Plants monopodial, each growth of indeterminate length; inflorescences lateral
6. Stems elongate; inflorescence more than 6 cm long; flowers pink or white ..... 25. ***Robiquetia***
6. Stems very short; inflorescence less than 6 cm long; flowers pale yellow ..... 26. ***Tuberolabium***