

Defining Generic Limits in



Trigonidium insigne



Trigonidium egertonianum



Trigonidium egertonianum

“I do not profess to be able of myself to settle at present the true limits of what may be called the Maxillaridious division of Vandaeae; but, in order to assist others who may be working in the Orchidaceous mine, I will just put down what I at present think will be the genera to be referred to it.”

— John Lindley, 1843, Botanical Register.

IF ONE GOES ORCHID HUNTING IN the forests of Central or South America, odds are that one of the first orchids you will encounter will be a *Maxillaria* or one of its close relatives. Maxillarias comprise a large percentage of the Neotropical orchid flora, as well as being relatively common. However, putting a name on these plants has vexed botanists for centuries. The flowers are often not showy, and tend to be relatively monotonous in form. The most recent volume of *Genera Orchidacearum*, Volume 5, Part 2 (Pridgeon et al. 2009), and the *World Checklist of Selected Plant Families* utilize a major new reclassification of *Maxillaria* and relatives.

Orchids in a botanical garden usually are easy to identify because they frequently have neatly printed tags bearing the names of the plants. Orchids in the wild lack such conveniences, and assigning them to genus and species requires a good library, years of experience and the ability to silence dissenting opinions. During much of the last three centuries, orchid classification was based largely on subjective opinion of an expert, and experts often differed in which plant traits they thought were most important. In recent decades, DNA sequencing has provided a much more objective means of classifying plants. In our attempt to reclassify *Maxillaria*, we sequenced DNA from more than 600 individuals. The resulting orchid “tree” forms the basis for our reclassification. The DNA study was published in 2007 (Whitten et al. 2007), together with a companion paper dealing with nomenclatural transfers (Blanco et al. 2007). The traditional Maxillariinae sensu stricto¹ (or “core Maxillariinae”) is now divided into 17 genera and roughly 580 species, and new species continue to be described at a steady rate.

¹Latin for “in the strict sense” or the narrow definition of Maxillariinae. In *Genera Orchidacearum*, Volume 5, Part 2 (Pridgeon et al. 2009), Maxillariinae is broadened to include Lycastinae and Bifrenariinae.

First, the good news: several long-recognized genera survive with few or no changes in the new classification. These survivors included *Trigonidium* (seven spp.), *Cyrtidiorchis* (five spp.), *Cryptocentrum* (18 spp.), *Pityphyllum* (seven spp.), and *Heterotaxis* (13 spp.). The remaining mass of reorganized species is now divided into 12 genera: *Maxillaria* (200–250 spp.), *Camaridium* (~80 spp.), *Maxillariella* (~50 spp.), *Rhetinantha* (15 spp.), *Sauvetea* (15 spp.), *Mormolyca* (~25 spp.), *Christensonella* (12 spp.), *Mapinguari* (four spp.), *Inti* (four spp.), *Brasiliorchis* (13 spp.), *Ornithidium* (~60 spp.) and *Nitidobulbon* (three spp.). The bad news is that some of these genera remain difficult to distinguish from each other on the basis of floral morphology alone.

When we began to study maxillarias, we started building a living collection, and eagerly sent photographs of the flowers to various Neotropical orchid experts for identification. We were immediately chastised for not sending images of the vegetative parts. Usually, flowers alone are insufficient to identify maxillarias and related genera; one must look at the whole plant, and pay careful attention to the diverse vegetative habits. Several morphological traits appear to be helpful in sorting out genera in Maxillariinae. Pseudobulbs may be present or absent. The pseudobulbs of some species are topped by a phyllopodium (“leaf foot”), a narrow projection that elevates the abscission layer of the leaf (where it breaks off upon drying) above the top of the pseudobulb. Flowers may arise from the most recent growths (either during its early development or after it matures), or they may be produced from the rhizome a few shoots behind the most recent growth. The sepals and petals may be tough and full of stringy fibers (readily visible when torn, like celery), or fibers may be absent (sepals tear cleanly). The capsules may open laterally, with slits in the capsule

Maxillaria

A Return to the Orchidaceous Mine

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Cyrtidiorchis alata — Habit and flower



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Cyrtidiorchis frontinoensis

walls, or the mature capsules may open at the apex, with the segments reflexing widely. Roots may be smooth, or they may bear ringlike thickenings. The flowers may have a prominent column foot (a chinlike hinge formed by fusion of the lip base and column extension), or the column foot may be absent. The lip may be simple and linear, or it may have prominent lateral lobes. The bract subtending the flower may be short or long. Finally, the presence/absence and type of floral reward for pollinators varies greatly among genera. These include nectar, resin (collected by female bees to build nests), pseudopollen (powdery fake pollen on the lip, collected by female bees to feed to larvae), or more commonly, no reward at all. In the latter category, the flowers can falsely advertise the presence of nectar, resin, or pollen rewards, or even mimic the females of their insect pollinators.

SMALLER GENERA Let's first discuss some of the smaller genera that are easily distinguished before examining the larger, more difficult genera.

TRIGONIDIUM Plants of *Trigo-*

nidium are either cespitose (with tightly clustered pseudobulbs) or long-rhizomatous, with pseudobulbs widely spaced along a thick rhizome. The ridged pseudobulbs have one to four apical leaves and are subtended by nonfoliaceous bracts. The inflorescences are erect, often long and wiry, and emerge from the most recent pseudobulbs. The flowers are erect and campanulate and lack a column foot. The sepals form a cup around the smaller petals and lip and are reflexed at the middle, giving the flowers a tuliplike appearance. The petals have characteristic shiny brownish- or bluish-metallic thickenings (glands?) at the apex. The capsules have lateral dehiscence. *Trigonidium* has been consistently recognized as a genus since its creation. The floral odors attract small bees that attempt copulation with the tiny lip enclosed by the sepals and petals (Singer 2002).

CYRTIDIORCHIS *Cyrtidiorchis* is a small high-elevation Andean genus with a dimorphic growth habit; juvenile plants have clustered pseudobulbs, but as they mature they produce monopodial branched canes. Inflorescences are supra-axillary² and are only produced by the adult shoots. The open, flat flowers are dull colored and lack fibers. The lip is minutely hairy and vaguely insectlike, and we suspect the flow-

ers are pollinated by pseudocopulation. The column is strongly arched, and the capsules have lateral dehiscence.

CRYPTOCENTRUM *Cryptocentrum* has long been recognized as a distinct genus. Plants of most species produce monopodial shoots; some resemble small *Aeranthes* plants while some others form small tufted rosettes that resemble a small *Tillandsia* (in the Bromeliaceae or pineapple family). Still others have tiny pseudobulbs and have sympodial growth. The inflorescences are often long and wiry, bearing small star-shaped, flat greenish flowers with a long spur concealed by the floral bract. The flowers are sweetly fragrant at night, produce nectar and are thought to be pollinated by small moths. Capsules have apical dehiscence. The molecular data show that *Anthosiphon roseans* (with pinkish-white flowers and small pseudobulbs) is closely related to *Cryptocentrum*, so we have lumped this single aberrant species into *Cryptocentrum*. The presence of greenish, star-shaped flowers with a long nectar spur is unique within core Maxillariinae.

PITYPHYLLUM Very distinctive, *Pityphyllum* has long been recognized as a separate genus. It is restricted to high-elevation Andean cloud forests where the plants form sprawling mats in exposed

²Emerging a few centimeters above the insertion point of the leaf in the middle of the internode. In most orchids (and most other plants), inflorescences arise strictly on the leaf axil.



Cryptocentrum latifolium



Cryptocentrum pseudobulbosum



Cryptocentrum roseans



Cryptocentrum standleyi



Pityphyllum saragurensis



Pityphyllum laricinum



Heterotaxis sessilis — Habit and detail of lip

trees. The tiny pseudobulbs are widely separated on long, flexible rhizomes, and the pseudobulbs are completely covered by and fused to a papery, brown subtending sheath (a tunica). Each pseudobulb can have from one to as many as 20 apical leaves that are thin and needlelike in some species but thick and fleshy in others. The apex of the leaf sheath bears a pair of thin brown projections (ligules) just below the abscission layer of the leaf. The presence of the tunica and the ligules defines the genus; no other genus in the Maxillariinae has these traits. The flowers are usually tiny and white to yellow, with narrow segments. The DNA data (together with the morphological traits of tunica and ligules) showed that *Maxillaria huancabambae* and *Maxillaria saragurensis* should be transferred into *Pityphyllum* (Whitten et al. 2006). This article by Whitten et al. (2006) also includes photographs of several species.

HETEROTAXIS Most species of *Heterotaxis* have laterally compressed, aggregated, oblong, unifoliate pseudobulbs subtended by several leaflike sheaths. *Heterotaxis equitans* and *Heterotaxis valenzuelana* have pseudomonopodial growths with thick leaves that lack pseudobulbs. The fleshy, yellowish, bell-shaped flowers have tough fibers in the sepals and petals and a very short column foot. The labellum has a pad of very short, glandular trichomes that likely constitute a reward for pollinators. The capsules have lateral dehiscence.

INTI The genus *Inti* presently consists of two species: *Inti bicallosa* and *Inti chartacifolia*. They are easily distinguished from all other genera by the fanlike growths of narrow, thin leaves and absence of pseudobulbs; superficially, they resemble a plant of *Pescatorea* or *Huntleya*. The small flowers have a linear callus of glandular hairs that might constitute a reward for small bees. The flowers have a fetid odor, much like a ripe cheese. Capsules are long and narrow with lateral dehiscence. Two species of *Maxillaria* recently described by Eric Christenson, PhD (2009) — *Maxillaria foetida* and *Maxillaria janicae* — need to be transferred to *Inti*, raising the total to four species.

NITIDOBULBON Only three species are in the genus *Nitidobulbon*: *Nitidobulbon cymbidioides*, *Nitidobulbon nasutum* and *Nitidobulbon proboscideum*. The generic name refers to the shiny, varnished surface of the pseudobulbs, which are topped by one or two leaves and several pairs of subtending bracts. A column foot is very short, and the linear lip bears a callus that secretes a sticky resin. The plants resemble those of the genus *Heterotaxis*, but the pseudobulbs of *Nitido-*



Inti bicallosa — Habit and inflorescence



Nitidobulbon proboscideum



Christensonella uncata



Christensonella vernicosa



Christensonella nardoides



Mapinguari desvauxianus — Habit and flower



bulbon have a lustrous, shiny texture (while those of *Heterotaxis* are matte).

CHRISTENSONELLA *Christensonella* is named for Eric Christenson, PhD, a noted *Maxillaria* specialist; the genus was investigated in detail by Koehler et al. (2007). This genus has long been recognized as a distinct group, often informally called the “*Maxillaria madida* alliance.” The small, tufted plants are mostly restricted to Brazil, but one species (*Christensonella uncata*) is widely distributed in tropical South and Central America. The leaves are often thick, succulent and tough or needlelike, and the flowers are usually tan to yellow to dark red and bear a shiny callus with no floral reward. The most distinguishing characteristic for *Christensonella* is the presence of warty, annular (ringlike) thickenings on the roots of most species; all other Maxillariinae have smooth roots.



Brasiliorchis phoenicanthera



Brasiliorchis schunkiana

MAPINGUARI *Mapinguari* is named for a mythical manlike beast of the Amazonian forest, and its four species occur in northern South America and southern Central American forests. Examples are *Mapinguari auyanepuiensis* and *Mapinguari longipetiolatus*. The pseudobulbs are tightly clustered and bear a single, narrow leaf, often with a long petiole. The most distinctive features are the small, reddish-brown flowers that are tightly clustered among the pseudobulbs, rarely exceeding the top of the pseudobulbs. The shiny callus of the lip bears no reward. Capsule dehiscence is lateral.

BRASILIORCHIS *Brasiliorchis* has long been recognized as the distinctive *Maxillaria picta* alliance (*Maxillaria* section *Repentes*). The tough, furrowed pseudobulbs are topped by a pair of leathery leaves, and their base is covered by papery bracts. Roots are relatively thick and smooth, and often tinged with purple. The flowers are borne on relatively tall scapes, and are cream color or pale yellow and spotted with red-purple; the spots are more intense on the exterior (abaxial) surface. The sepals and petals lack fibers, and the flowers bear no reward; capsules have apical dehiscence. As the name implies, the group is largely restricted to Brazil.



Sauvetrea aff. *alpestris* — Habit and flower



SAUVETREA *Sauvetrea* (*Maxillaria* section *Trigonae*, or the *Maxillaria alpestris* alliance)³, was named by Szlachetko

³*Maxillaria* section *Trigonae* became *Sauvetrea*, but authors differ on what species should be included in this group. According to the DNA data, some species that Szlachetko included in *Sauvetrea* do not belong there, and should be placed in other genera. It depends on what species he chose as the type species for the genus, and which species cluster together with it, according to the DNA.

and Smiszek (2007), but these authors included a hodge-podge of unrelated species that was later clarified by DNA data. The ribbed, unifoliate pseudobulbs are often widely spaced on the rhizome. The flowers emerge from the base of the still-developing pseudobulbs. Flowers have a very short column foot and lack fibers and produce no obvious secretion. The lip is three-lobed, with the midlobe much longer than the lateral ones. The most distinctive feature of this genus is the strongly three-ribbed capsule (hence the name *Trigonae*); even the ovary of the flower is triangular in cross-section.

RHETINANTHA Plants of *Rhetinantha* bear ribbed pseudobulbs with two–four apical leaves, often widely spaced on the rhizome, but the flowers emerge from the base of the most recent growth. The lip is simple and lacks lateral lobes. “Rhetinantha” means “resin-flower,” and all species in this group bear one or more distinct glands on the lip that secrete a sticky resin or crystalline wax. *Rhetinantha acuminata* and *Rhetinantha notyloglossa* bear especially prominent waxy deposits on the lip; these waxes or resins are probably collected by female bees and used to construct the walls of their nest. One aberrant species is *Rhetinantha witse-nioides*, which has a long (to 39 inches [1 m]) pendent, monopodial stem covered with equitant glaucous leaves, and is superficially similar *Heterotaxis valenzuelana*. The latter species also has glaucous leaves, but the yellow flowers do not produce any resin.

MORMOLYCA Traditionally, *Mormolyca* consisted of a few species that bear wiry inflorescences with flowers having a vaguely insectlike lip. Studies by Rodrigo Singer (Singer et al. 2004) demonstrated that the flowers of *Mormolyca ringens* produce a pheromonelike odor that attracts male stingless bees, and the bees attempt to copulate with the flowers (much like in European *Ophrys*). Pseudocopulatory pollination is also suspected in the genus *Chrysocycnis*. Surprisingly, the DNA data showed a close relationship between *Mormolyca*, *Chrysocycnis* and the species of *Maxillaria* section *Rufescens*. Consequently, Mario Blanco and I decided to lump all three of these taxa into a single genus, for which *Mormolyca* is the oldest name. Although lumping these species with insectiform lips and pseudocopulation together with *Maxillaria* section *Rufescens* may seem discordant, they actually share several traits. All bear lips with a long midlobe and (usually) pointed acute side lobes. Most species of *Maxillaria* section *Rufescens* have potent, diverse floral fragrances, and this may have predisposed some species



Rhetinantha scorpioidea — Habit and resin on lip



Mormolyca sp. — Position of inflorescence



Mormolyca richii



Mormolyca ringens



Mormolyca schweinfurthiana



Ornithidium fulgens — Habit and inflorescence



Ornithidium nubigenum



Ornithidium sophronitis



Ornithidium canarense

to evolve the production of fragrances that mimic the pheromones of female bees. The usually unifoliate pseudobulbs have a minutely warty, wrinkled texture, and the inflorescences usually arise from the rhizome between older bulbs (not from the current growth). The column is thick and curved (arcuate). The column foot is very short, the sepals and petals lack fibers, and the capsules have apical dehiscence.

LARGEST GENERA Remaining are the four largest genera: *Ornithidium*, *Maxillaria*, *Camaridium* and *Maxillariella*.

ORNITHIDIUM The name *Ornithidium* means “bird-flower”; many species in this genus are adapted for pollination by hummingbirds. Although the flowers are small, they are often produced in large clusters (fascicles) with bright red, yellow or orange pigments. To reward the visiting hummingbirds, they often produce abundant nectar. The pedicel and ovary are much longer than the subtending floral bract. Thick floral segments and a lip that is rigidly attached to the column protect against the bird’s probing bills (although the flowers lack fibers), and the pollinaria are relatively tiny (an adaptation thought to reduce the likelihood that the birds will see pollinaria on their bills and wipe them off). Many other species, however, have inconspicuous greenish flowers that are probably pollinated by insects. Species of *Ornithidium* can be either sympodial (cespitose [tufted] to long-rhizomatous) or monopodial; a few species (e.g., *Ornithidium miniatum*) have dimorphic growth (sympodial juvenile shoots and monopodial adult shoots; i.e., young plants have clustered pseudobulbs, but adult plants may have only tall canes).

The stems and leaves of most species have an olive green coloration, which is persistent on drying. When present, the ovoid pseudobulbs have a shiny, minutely cracked texture reminiscent of old varnish. The thick roots have a characteristic orangish coloration. Capsules have apical dehiscence. Examples include *Ornithidium aureum* (tall canes with globose yellow flowers) and *Ornithidium sophronitis* (small repent [creeping] plants with pseudobulbs and bright red flowers).

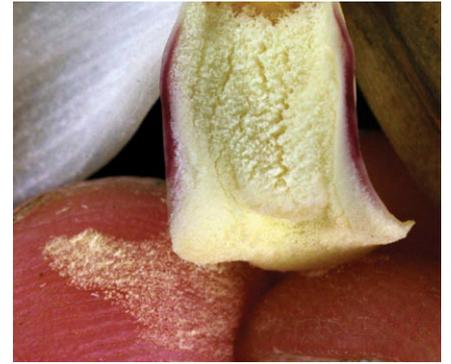
MAXILLARIA By far the largest number of species is in *Maxillaria* (mostly in South America) as well as the largest, most showy flowers, and consequently the genus is the most interesting to orchid growers. As circumscribed here, true maxillarias nearly always have cespitose pseudobulbs; the exceptions are species related to *Maxillaria exaltata*, which have tall, narrow canes. The pseudobulbs almost invariably are unifoliate, smooth and laterally compressed, with subtending sheaths that are often large and



Maxillaria fletcheriana



Maxillaria grayi



Maxillaria grayi — Pseudopollen on lip

leaflike. The abscission layer of the apical leaf is often projected above the pseudobulb in a persistent stalk (phyllodium); phyllopodia occur only in *Maxillaria*, and never in other genera of the subtribe Maxillariinae. The inflorescences always emerge from the base of the youngest pseudobulbs (from the leaf axils near the top of the stem in the *Maxillaria exaltata* alliance). The floral bract can be shorter or longer than the pedicel and ovary. The flowers have a prominent column foot and a hinged, flexible lip, and abundant, tough, perianth fibers. None of the species produce nectar, but many produce pseudopollen, a floral attractant not found in any other genus of the subtribe. The erect capsules have lateral dehiscence. Examples of true maxillarias are *Maxillaria grandiflora*, *Maxillaria fletcheriana* and *Maxillaria splendens*.

CAMARIDIUM Central America is the center of diversity for *Camaridium*. Species of *Camaridium* are variable in growth habit; most have pseudobulbs separated by rhizome segments of variable length. Some species are caespitose, and others lack pseudobulbs completely and have monopodial shoots (canes). A few species (e.g., *Camaridium inauditum*) have dimorphic growth (juvenile sympodial shoots with tightly spaced pseudobulbs, and monopodial mature shoots without pseudobulbs). In all species, the floral bract is longer than the pedicel and ovary, and the bract overlaps with the base of the dorsal sepal (this feature is useful in separating *Camaridium* from *Maxillariella* and *Ornithidium*). The column foot can be short or long. The sepals and petals lack fiber bundles and have a sparkling, crystalline appearance (due to minute bumps [papillae] on the epidermal cells). Most species appear to have deceptive flowers, but some produce nectar. The pendent fruits have apical dehiscence. Examples of *Camaridium* include *Camaridium scalariforme*, *Camaridium horichii* and *Camaridium ctenostachys*.

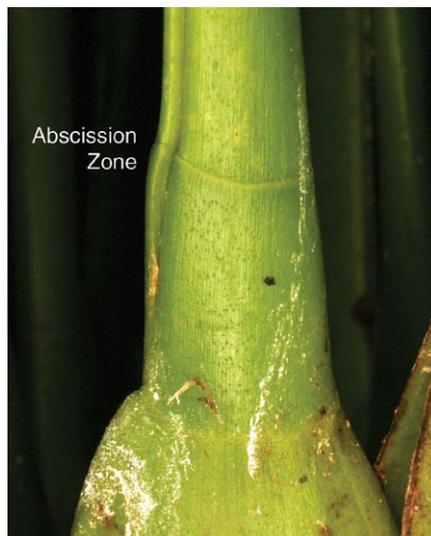
One of the most distinctive groups within *Camaridium* is the taxonomically



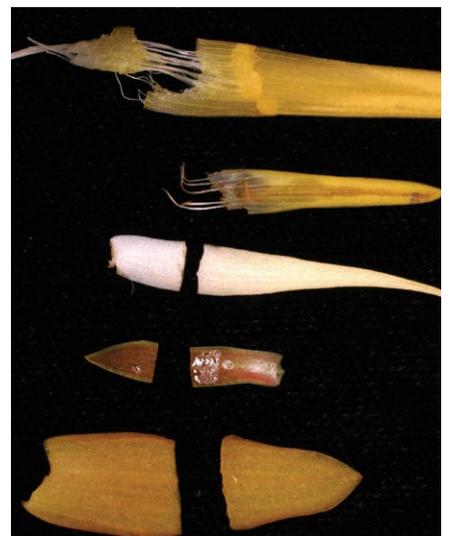
Maxillaria angustisegmenta



Maxillaria platypetala



Maxillaria plant showing the leaf base (petiole) with the abscission layer elevated above the top of the pseudobulb, forming a phyllopodium. Within the Maxillariinae, only true *Maxillaria* species possess a phyllopodium.



Torn sepals of five species, showing the presence or absence of tough fiber bundles. Top to bottom: *Maxillaria gentryi*, *Maxillaria ochroleuca*, *Camaridium ctenostachyum*, *Camaridium hoehnei* and *Mormolyca rufescens*.



Camaridium bradeorum



Camaridium inauditum



Camaridium densum — Habit and inflorescence



Camaridium scalariforme

difficult *Camaridium cucullatum* complex. This clade is sister to the rest of *Camaridium*, and could be split off as a separate genus that would bear the existing name *Psittacoglossum*. This generic name is apt, because species of this group have a lip that does bear a strong resemblance to the fleshy tongue of a parrot.

MAXILLARIELLA Species of *Maxillariella* are variable in terms of growth habit, but most have pseudobulbs separated by medium to long rhizome segments. The ovoid pseudobulbs are either uni- or bifoliate. Several species with long rhizomes have foliaceous bracts covering the segments between pseudobulbs. Others have pseudobulbs reduced or even absent, and these species show a clear gradient from sympodial to monopodial growth. The most derived members of this genus (*Maxillaria* section *Ebulbes* or the “*Maxillaria graminifolia* suballiance”; Atwood 2003) have thin, wiry, monopodial stems completely devoid of pseudobulbs, and narrow, acute leaves. Invariably, only one flower is produced from each leaf or bract axil (e.g., the inflorescences are not fasciculate nor produced sequentially), and the floral tract is shorter than the pedicel and ovary. The column foot is very short, and the labellum is simple or obscurely three-lobed and has a glossy, often reddish callus. The flowers mostly seem to be deceitful, promising resin or nectar that is not really there. The capsules have lateral dehiscence. Examples include *Maxillariella tenuifolia*, *Maxillariella anceps* and *Maxillariella sanguinea*.

Why is this new classification system an improvement over the old ones? The answer is simple: the new system makes the generic names much more predictive of plant traits. For example, under the old system, if you told me that you had a plant of *Maxillaria*, I would not be able to predict anything about its growth habit, the capsule type, the floral rewards, the presence or absence of fibers, the number of flowers per node, where the inflorescences arise, or its geographic distribution. On the other hand, if you tell me that you have a plant of *Christensonella*, I immediately know that this is a small, tufted plant probably from Brazil that would fit in a teacup, that it has small flowers that lack any reward, and that the capsules have apical dehiscence and the roots bear ringlike thickenings. Also, I would know that it is one of only 13 possible species, instead of one of more than 600. These new generic names carry much more information about the plants than did the old names.

So, with all these changes in generic names in the *Maxillaria* subtribe, how does one know what name to write on your

plant tags or show registrations? Usually, we don't know if the plant has capsules with lateral or apical dehiscence, and most growers are reluctant to tear a flower apart to see if it has tough fibers in the sepals and petals. Fortunately, if you know the traditional name for your plant, you can go to the *World Checklist of Selected Plant Families* (<http://apps.keew.org/wcsp/home.do>) and enter the name, and it will give you the currently accepted genus and species. For example, if you search for *Maxillaria cucullata*, it will give you the accepted name, *Camaridium cucullatum* (Lindl.) M.A. Blanco. Some species of uncertain affinity (based on their morphology) still have not had their DNA analyzed to verify their generic placement, but these are rarely (if at all) found in cultivation anyway.

We now have an objective generic classification that breaks *Maxillaria* up into manageable and monophyletic units, and this paves the way for more intensive detailed studies of each genus. Indeed, Rafael Arevalo, a PhD student working under Ken Cameron, PhD, at the University of Wisconsin–Madison, is studying this re-defined *Mormolyca* for his dissertation. All of the genera need more detailed study, and we have set the stage for the next generation of orchid biologists.

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Maxillariella elatior



Maxillariella guareimensis



Maxillariella tenuifolia



Maxillariella vulcanica

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