

# Genera *Zygopetalinarum*

## Part 2: The genus *Cochleanthes*

FRANCO PUPULIN describes *Cochleanthes aromatica* and *C. flabelliformis*

**C**OCHELEANTHES RAF. has historically been a sort of 'accordion' genus in the *Orchidaceae*. Originally created to embrace a single, aberrant 'Zygopetalum' species from Jamaica (Rafinesque 1836), it grew to include about 15 species of non-pseudobulbous

*Zygopetalinae* (Schultes & Garay 1954, Garay 1969). Today's classification, aimed to circumscribe monophyletic genera on the basis of phylogenetic reconstruction, favours a narrow definition of *Cochleanthes*, only encompassing two widely distributed species (Whitten *et al* 2005).

### First species

The first species of this genus appeared in 1788, in the *Prodromus* of Olof Swartz's treatment of the gynandrous orchids for the flora of the West Indies. Here, within the section of the acaulescent epidendrums, with leaves produced



**Above:** *Zygopetalum gibezae* as originally illustrated in *Lindenia* in 1888, on the basis of a plant of unknown locality

**Left:** The original illustration of *Zygopetalum cochleare*, from the *Botanical Register*, based on a specimen native to Trinidad

'from the roots', Swartz described his *E. flabelliforme*, characterised in a short diagnosis as a single-flowered species, provided with ovate-lanceolate, acute leaves (Swartz 1788).

Swartz moved *E. flabelliforme* to *Cymbidium* in 1799 (Swartz 1799), and in his *Flora Indiae Occidentalis* he provided an augmented and improved description of the species (Swartz 1806: 1471). Notwithstanding Swartz's more detailed characterisation, the 'flabelliform' orchid from Jamaica was, in fact, overlooked up to 1863, when HG Reichenbach recognised the close relationship of *Epidendrum flabelliforme* to *Zygopetalum* Hook., and transferred it to that genus as *Z. flabelliforme* (Sw.) Rchb. f.

Meanwhile, in 1836, John Lindley described *Zygopetalum cochleare*, or the

'spoon-lipped zygotepetalum', in the *Botanical Register*, based on a specimen from Trinidad flowering in the collection of Mr Knight (Lindley 1836) (see fig p202). The plant, stated to be 'the most attractive upon the whole [*Zygopetalum*]' (Lindley 1836), was finely illustrated by the enigmatic Miss E Drake (Cribb 1991) under plate 1857.

Lindley mentions the 'rich Lapis lazuli blue' veining of the lip together with the rounded, convex, many-cristate callus and the delicious fragrance of the flower. Apparently, however, not all specimens of the flabelliform *Cochleanthes* have scented flowers, and both Fowlie (1961) and Ackerman (1995) recorded non-fragrant, self-pollinating plants from the Greater Antilles.

### Selecting the type

Also in 1836, the Turkish botanist and professor of natural history in the United States, CS Rafinesque-Schmalz, noted that *Zygopetalum cochleare* was distinct enough from *Zygopetalum* to deserve a genus of its own, and in his *Flora Tellurica* he selected Lindley's *Z. cochleare* as the type of the new genus *Cochleanthes*, proposing for it the new specific epithet *fragrans*, in reference to the species' sweetly scented flowers (Rafinesque 1836). ➤

**Below left:** *Cochleanthes flabelliformis*, illustrated as *Zygopetalum cochleare* in Curtis's *Botanical Magazine* of 1838 (pl.3585)

**Below:** A copy of the original watercolour of *Zygopetalum wendlandii*, prepared for Prof Oakes Ames at the Reichenbach Herbarium, now kept at the Oakes Ames Orchid Herbarium. Reproduced with the kind permission of the Director, Harvard University Herbaria



The generic name was derived from the Latin *cochlea* = shell, in allusion to the cochleate lip and its shell-shaped callus. However, due to the limited circulation of Rafinesque's work, the name *Cochleanthes* rapidly fell into botanical oblivion. It was not until more than a century later that it was resurrected by Schultes and Garay (1959) for nomenclatural purposes. By that time, more superfluous names had been published for the fan-shaped *Cochleanthes*.

### *Zygopetalum gibeziae*

In 1888, when the mania of orchid cultivation had reached its peak, leading to the publication of several beautifully illustrated magazines, the species was described by NE Brown in *Lindenia* as *Zygopetalum gibeziae* (see fig p202), the specific epithet honouring, on request by J Linden, Mrs Gibez for her renowned orchid collection (Brown 1888). A few years later, in his *Orchideenbuch*, Stein (1892) moved the species to *Warczewiczella*. The true phylogenetic relationships of the fragrant, blue-lipped 'zygopetalum' from the West Indies remained obscure for a long time.

Ernst Gottlieb von Steudel treated Lindley's *Zygopetalum cochleare* as a member of the genus *Eulophia* (synonymised by Hooker 1838 (see fig p203)). Some years later Reichenbach moved it to his genus *Warczewiczella* (Reichenbach 1852), reducing into synonymy of this species the name of *Huntleya imbricata* by which it had been known in horticultural circles. The '*Epidendrum*' or '*Cymbidium*' described by Swartz had a similar destiny, and in 1903 Cogniaux named it *Warczewiczella flabelliformis*.

### *Zygopetalum aromaticum*

The second species of the genus was originally described by Reichenbach in 1852 as *Zygopetalum aromaticum*.

In the protologue, Reichenbach provided a detailed description of the semilunate, plurisulcate callus, apically 'flushing' into the lamina, which is characteristic of *Cochleanthes*. The type specimen was originally collected somewhere in 'Mittelamerika' (ostensibly, in Costa Rica or Panama, where the species is endemic), but in Reichenbach's herbarium in Vienna I was unable to find a specimen that could be referred to this collection unequivocally. Among the material annotated by Reichenbach as '*Zygopetalum aromaticum*', both plants from Costa Rica (*Endrés 201*, *Endrés s.n.*) and Panama (Chiriquí, Volcán, without collector) are still in existence.

In 1866 Reichenbach described the same species again, with the name *Zygopetalum wendlandii* (see fig p203), on the basis of a plant collected by Herman Wendland along the lower slopes of the Irazú volcano in Costa Rica, and flowered in the 'Costa Rica-Haus', expressly created for his Central American collections in the renowned gardens of Herrenhausen.

Both of Reichenbach's 'zygopetalums' were moved up and down among the genera of *Zygopetalinae*. Before Schultes and Garay (1959) formally assigned *Zygopetalum aromaticum* to *Cochleanthes*, the species was transferred by Reichenbach (1852) to *Warczewiczella*, and by Allen (1949) to the genus *Chondrorhyncha*. *Zygopetalum wendlandii* also found its way to *Warczewiczella*, where it was placed by Schlechter in 1918.

### Flower morphology

In reviving *Cochleanthes*, Schultes and Garay (1959) assigned to that genus all the species previously described under *Warczewiczella* Rehb. f., but the morphology of the flower is rather different in the two groups.

The latter genus was revised in

1969 by Fowlie, who distinguished it from *Cochleanthes* on the basis of the lip callus, free laterally and at the apex (versus solidly attached to the labellum at the base, in front and laterally in *Cochleanthes*) and composed of radiating, digitate 'promontories' (vs a series of adjacent plates distally attached to the lip), the abruptly reflexed lateral sepals (vs gently curved forwards) and the lack of a longitudinal, ventral keel on the column (prominent in *Cochleanthes*).

Nevertheless, in his revision of the *Chondrorhyncha* complex, Garay (1969) maintained a wide concept of the genus *Cochleanthes*. Here, among the species lacking pseudobulbs, provided with an entire lip articulated to the column foot, a three-lobed rostellum, and a column not keeled in front, he mainly distinguished *Cochleanthes* from *Chondrorhyncha* by the short column-foot forming an obtuse (vs acute) mentum, and the basal callus (vs placed in the centre of the disc).

This view prevailed in taxonomic literature (Rodríguez Caballero *et al* 1986, Werkhoven 1986, Senghas 1990, Senghas and Gerlach 1991, Mora-Retana and Atwood 1992, Mora-Retana and García 1992, Christenson 1997, Rungius 1998, Cavestro and Roucoule 2003, among others) until today.

However, recent studies based on comparison of DNA sequences (Whitten *et al* 2005) show that *Cochleanthes* is only distantly related to *Warczewiczella*, as was previously suggested by Fowlie. As currently understood, the genus can be characterised by the relatively large plants and flowers, the lip flat or only slightly concave, not enfolding the column, provided with a rounded, multiseriate callus, laterally fused with the lip, and the column with a ventral keel (Dressler 2000, Pupulin 2005, Whitten *et al* 2005).



**Above:** *Cochleanthes aromatica*, a specimen without collection data, flowered in cultivation at Jardín Botánico Lankester, 8 May 2002. Reproduced with the kind permission of the University of Costa Rica Press

**Above right:** *Cochleanthes aromatica*, a specimen from the premontane wet forest of central Pacific Costa Rica *Pupulin et al 3010*, (Jardín Botánico Lankester-Spirit)

### Taxonomy

*Cochleanthes* Raf.,

*Flora Tellurica* 4: 45. 1836

Type: *Cochleanthes fragrans* Raf., nom. illeg. (*Zygopetalum cochleare* Lindl.) = *Epidendrum flabelliforme* Sw.

Syn: *Zygopetalum* Hook. sect.

*Cochleare* Rchb. f., Walp. Ann. Bot. Syst. 6: 682. 1853.

A genus of two species ranging from Mexico and the West Indies to northern South America.

1 *Cochleanthes aromatica* (Rchb. f.) Schultes & Garay, Bot. Mus. Leaf.

Harvard Univ. 18: 323. 1954. Fig 5–8  
Syn: *Zygopetalum aromaticum* Rchb. f., Bot. Zeit. (Berlin) 10: 668. 1852.

*Warczewiczella aromatica* (Rchb. f.) Rchb. f., Walp. Ann. Bot. Syst. 6: 654. 1852. *Cbondrorhyncha aromatica* (Rchb. f.) P H Allen, Ann. Missouri Bot. Gard. 36: 85. 1949

Type: 'Mittelamerika' (W, not located) *Zygopetalum wendlandii* Rchb. f., Beitr.

Orch. Centr.-Amer. 74. 1866. *Bollea wendlandiana* hort. ex Gard. & For. 1: 315. 1888.

*Warczewiczella wendlandii* (Rchb. f.) Schltr., Beih. Bot. Centralbl. 36(2): 494. 1918.

Type: Costa Rica: in montis Irazú [Irazú volcano] pede, ex horto Herrenhusano, *H. Wendland s.n.* (W *Rchb-Herb!*).

**Plant** epiphytic, caespitose, without

pseudobulbs (rarely with very small pseudobulbs completely hidden by the leaf bases), the abbreviated stem with 6–7 imbricating sheaths, the upper ones foliaceous.

**Leaf** conduplicate, articulate, membranaceous, oblanceolate to narrowly elliptic-obovate, acute, abaxially keeled, narrowed at the base into a indistinct, conduplicate

petiole, grass-green, 18–40 x 2–5cm. **Inflorescence** lateral, stout, from the axil of the lower sheaths, 1-flowered; peduncle terete, suberect, to 15cm.

**Floral bract** double, conduplicate, the external one loose, broadly ovate, the sub-opposite internal bractlet ligulate.

**Ovary** pedicellate, terete, to 2.7cm including the pedicel. **Flower** large, strongly and sweetly scented, the sepals and petals pale greenish cream to pale green, the lip whitish cream with a large, violet-purple median band, the callus white. **Dorsal sepal** free, lanceolate-elliptic, acuminate, slightly reflexed at the base, 45–55 x 13–16mm. **Lateral sepals** basally adnate to the column foot, lanceolate-elliptic, acute to acuminate, strongly reflexed-folded towards the base,

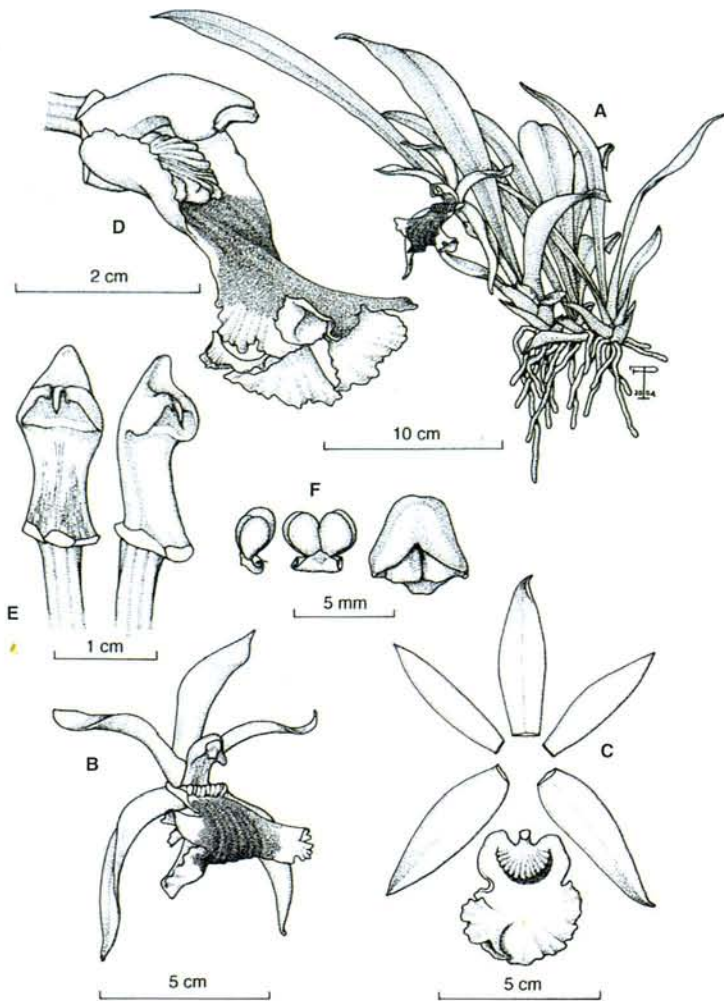
### KEY TO THE SPECIES OF COCHLEANTHES

1 Lip pandurate, distinctly 3-lobed, flat to slightly convex, with a single, large purple blotch in the centre

1a Lip suborbicular-flabellate, obscurely 3-lobed, concave at the base, with many radiating, violet stripes from the base, sometimes solidly violet-purple at apex

*C. aromatica*

*C. flabelliformis*



*Cochleanthes aromatica* (Rchb. f.) Schultes & Garay. A - Habit. B - Flower. C - Dissected perianth. D - Column and lip, lateral view. E - Column, ventral and three quarter view. F - Pollinarium (two views) and anther cap. Drawn by the author from Pupulin et al. 3010 (Jardín Botánico Lankester-Spirit)

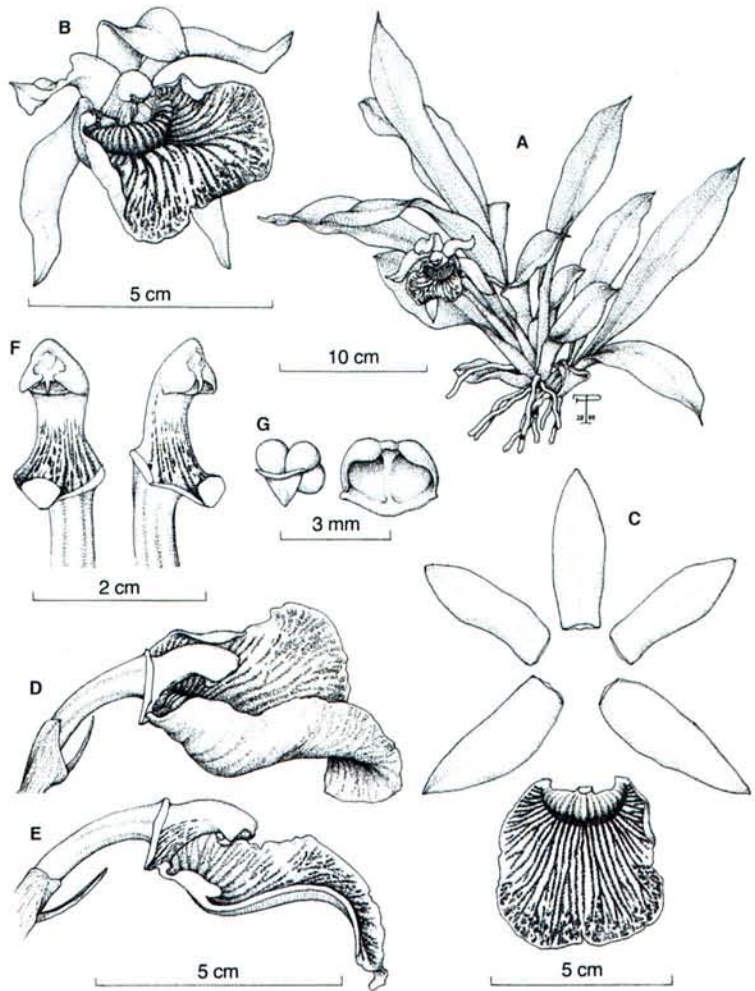
45–55 x 15–17mm. **Petals** obovate, acute, 40–45 x 9–11mm. **Lip** with a short claw, articulate with the column foot, three-lobed, pandurate, 40–45 x 28–38mm, the base cordate, notched-bilobed and often reflexed at apex, the apical margins strongly crisped; disc with a semilunate, multiseriate callus, composed of 14–18 low, radiating, rounded ridges, protruding apically into rounded keels, the central ones longer, c10 x 18mm.

**Column** slightly curved, clavate, c20mm long, with a transverse, narrow stigma, the ventral surface basally provided with a low, rounded keel. **Anther cap** cucullate, ovate, 2-celled. **Pollinia** 4, in 2 subequal pairs, on a elliptic-ovate, hyaline viscidium. Distribution: Costa Rica and Panama. Habitat and ecology: *Cochleanthes aromatica* is a relatively common epiphyte native to the warm, tropical and submontane wet forests of Costa

Rica and western Panama, at elevations between 400 and 1,200m. Flowering has been recorded from July–December, with a peak during September–October, corresponding to the rainiest months in the region.

**Notes**

According to Dressler (2000), the natural hybrid of *C. aromatica* with *Warczewiczella discolor* is infrequently found in Costa Rica; the flowers of the hybrid have a widely open lip, uniformly tinged with dark red or purple-red. *Cochleanthes aromatica* is pollinated by male euglossine bees of the genera *Euglossa* and *Eulaema*, on which the pollinarium is placed behind the head (van der Pijl and Dodson 1966); however, members of the related genus *Warczewiczella* also attract female eulaemas probing the funnel-shaped lateral sepals for food resources (Ackerman 1983).



Another form of *C. aromatica* with the lip almost completely white, originally collected in Costa Rica on the crest of Cerro Nara, at 1000m elevation (Pupulin et al 2092, Jardín Botánico Lankester-Spirit)

**2 *Cochleanthes flabelliformis* (Sw.) Schultes & Garay, Bot. Mus. Leaf. Harvard Univ. 18: 324. 1954. Fig 9–13 Syn: *Epidendrum flabelliforme* Sw., Nov. Gen. & Spec. Pl. Prodr. 123. 1788. *Cymbidium flabelliforme* (Sw.) Sw., Nov. Act. Upsal. 6: 73. 1799. *Zygopetalum flabelliforme* (Sw.) Rchb. f., Walp. Ann. Bot. Syst. 6: 652. 1863. *Cymbidium flabellifolium* Sw. ex Britt., Fl. Brit. West Ind. Isl. 629, 1864, *sphalm.* *Warczewiczella flabelliformis* (Sw.) Cogn., in Urban Symb. Antill. 4: 182. 1908. Type: Jamaica. 'Provenit rarius in arboribus montium Jamaicae,' Swartz s.n. (BM, UPS, not seen).**

*Zygopetalum cochleare* Lindl., Bot. Reg. 22: sub pl. 1857. 1836. *Cochleanthes*

*Cochleanthes flabelliformis* (Sw.) Schultes & Garay. A - Habit. B - Flower. C - Dissected perianth. D - Column and lip, lateral view. E - Column and lip, lateral view, the lip in longitudinal section. F - Column, ventral and three quarter views. G - Pollinarium and anther cap. Drawn by the author from Pupulin 5725 (Jardín Botánico Lankester-Spirit)

*fragrans* Raf., Fl. Tellur. 4: 45. 1836, *nom. illeg.* *Eulophia cochleata* Knight ex Hook., Bot. Mag. 64: sub pl. 3585. 1837. *Zygopetalum cochleatum* Paxt., Mag. Bot. 4: 279. 1838. *Warczewiczella cochlearis* (Lindl.) Rchb. f., Bot. Zeit. 10: 714. 1852. *Huntleya imbricata* hort. ex Rchb. f., Bot. Zeit. 10: 714. 1852, in *syn.* *Zygopetalum conchaceum* Hoffmanssegg ex Rchb.f., Bot. Zeit. 10: 714. 1852, in *syn.* *Warczewiczella cochleata* Barb. Rodr.,

Struct. des Orch. pl. 13, fig. 4. 1883. Type: Trinidad, cult. Knight s.n. (K, not seen).

*Warczewiczella cochlearis* (Lindl.) Cogn. var. *atroviolacea* Cogn., Dict. Ic. Orch., *Warczewiczella* pl. 1, fig. B. 1897. *Warczewiczella flabelliformis* (Sw.) Cogn. var. *atroviolacea* Cogn., Martius Fl. Bras. 3(6): 472, 1906. Type: Brazil? Cult. by A.-A. Peeters of St-Gilles-Bruxelles, 1897 (not seen). ➤



A specimen of *C. flabelliformis* from Cuba, originally collected on Pico Kentucky (Prov. Santiago de Cuba) and cultivated at Orquideario Soroa, flowered at Jardín Botánico Lankester, 25 Sept 2001 (F Pupulin 2594, Jardín Botánico Lankester-Spirit)



A Venezuelan plant of *C. flabelliformis*, without collection data, flowered in cultivation in the collection of Giancarlo Pozzi at Morosolo di Casciago, Italy, 20 August 2005 (F Pupulin 5727, Jardín Botánico Lankester-Spirit)



*Cochleanthes flabelliformis* (as *Warszewiczella cochlearis*) on the left, and the horticultural form *atroviolacea* Cogn. (right), illustrated in a fine watercolour by A Goossens in 1897

*Warszewiczella cochlearis* (Lindl.) Cogn. var. *marginata* Cogn., Dict. Ic. Orch., *Warszewiczella* pl. 1B, fig. 1. 1898.

*Warszewiczella flabelliformis* (Sw.) Cogn. var. *marginata* Cogn., Martius Fl. Bras. 3(6): 472, 1906.

Type: Cult. by A.-A. Peeters of St-Gilles-Bruxelles, 1897 (not seen).

*Warszewiczella cochlearis* (Lindl.) Cogn. var. *peetersii* Cogn., Dict. Ic. Orch., *Warszewiczella* pl. 1B, fig. 2. 1898.

*Warszewiczella flabelliformis* (Sw.) Cogn. var. *peetersii* Cogn., Martius Fl. Bras. 3(6): 472, 1906.

Type: Cult. by A.-A. Peeters of St-Gilles-Bruxelles, 1897 (not seen).

*Zygopetalum gibezeiae* N.E. Br., Lindenia 4: 79, pl. 181. 1888.

*Warszewiczella gibezeiae* (N.E. Br.) Stein, Orchideenb. 595. 1892.

Type: without locality, cultivated by Linden (not located).

**Plant** epiphytic or rarely lithophytic, caespitose, without pseudobulbs, the abbreviated stem with 6–7 imbricating sheaths, the upper ones foliaceous.

**Leaf** conduplicate, articulate, membranaceous, oblanceolate, acuminate, narrowed at the base into a indistinct, conduplicate petiole, grass-green, 16–30 x 3–5cm. **Inflorescence** lateral, stout, from the axil of the lower sheaths, 1-flowered; peduncle terete, spreading to suberect, to 10cm long.

**Floral bract** double, conduplicate, the external one broadly ovate, the internal bractlet narrowly lanceolate.

**Ovary** pedicellate, terete-subclavate, to 2cm long including the pedicel.

**Flower** large, strongly and sweetly scented or odourless, the sepals and petals pale green, the lip whitish cream, basally veined with violet or purple, apically sometimes solidly violet, the callus white spotted violet or purple. **Dorsal sepal** free, lanceolate-elliptic, acute, slightly reflexed at the

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base, 30–45 x 11–15mm. **Lateral sepals** basally adnate to the column foot, lanceolate, acute, strongly reflexed-folded toward the base, 30–48 x 13–17mm. **Petals** oblanceolate, acute, 27–38 x 11–15mm. **Lip** with a short claw, articulated to the column foot, obscurely three-lobed, suborbicular-flabellate, 38–42 x 40–45mm, the base cordate, notched-bilobed at apex, the apical margins undulate-crisped; disc

with a semilunate, multiseriate callus, composed of 15–17 low, radiating, rounded ridges, c10 x 25mm. **Column** slightly curved, dilated at apex into rounded stigmatic wings, c15mm long including the foot, with a transverse, narrow stigma, the ventral surface basally provided with a low keel. **Anthercap** cucullate, transversely elliptic, 2-celled. **Pollinia** 4, in 2 subequal pairs, on a triangular, hyaline viscidium.

Distribution: Cuba, Jamaica, Puerto Rico, Dominican Republic, Trinidad, Mexico, Honduras, Nicaragua, Colombia, Ecuador, Venezuela, Brazil. Habitat and ecology: An epiphyte growing in shade in tropical to submontane wet forests at 200–1,000m elevation. Self-pollinating forms are more frequent in the West Indies, whereas in Central and South America the plants are usually





*Cochleanthes flabelliformis* var. *marginata* Cogn. and var. *peetersi* Cogn., both flowered in the collection of M. A.-A. Peeters at St-Gilles-Bruxelles, illustrated in 1898 in the *Dictionnaire Iconographique des Orchidées*

cross-pollinating. Flowering occurs from August to November.

### Notes

The species is apparently rare in Mesoamerica. Three unvouchered observations were made by Heller in widely separated areas of Nicaragua (Hamer 1982: sub pl. 638), but no records are known from southern Central America, namely from Costa Rica and Panama. According to Ackerman (1995), populations of *C. flabelliformis* from Puerto Rico lack any fragrance, and the self-pollinating flowers do not open fully. A high rate of fruit production, pointing to self-pollination, was also observed by Fowlie (1961) in populations from Jamaica. According to Cogniaux

(1897), the form with a solid violet-purple lip apex (see fig above) was originally introduced by Knight in 1835–1836 from the States of Sao Paulo and Minas Geraes in Brazil; other specimens were collected by Wagener in Venezuela, in the vicinity of Caracas, and supposedly in Trinidad.

### Cultivation

Information on cultivation was included in 'The genus *Cochleanthes* Raf', by William Cavestro & Denise Roucoule, *The Orchid Review*, Sept/Oct 2003, pp281–286. ■

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### GLOSSARY

adnate	attached to
caespitose	tufted
clavate	club-shaped
conduplicate	folded
cucullate	hooded
cuneate	wedge-shaped
flabellate	fan-shaped
foliaceous	leafy
heteroblastic	having pseudobulbs of one internode
homoblastic	having pseudobulbs of several internodes
hyaline	translucent
imbricate	overlapping
ligulate	strap-shaped
monophyletic	a group including all the descendants of a common ancestor
multiseriate	arranged in several parallel rows
pandurate	fiddle-shaped
pedicel	the stalk of an individual flower
peduncle	the stalk of an inflorescence
petiole	leaf stalk
polyphyletic	a group derived from different ancestors
retuse	notched
terete	cylindrical

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