

SYSTEMATICS AND THE SEGREGATION OF *ENCYCLIA*¹

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ABSTRACT: Previous taxonomic treatments of *Encyclia* (a series of lumping and splitting events) have resulted in a complex succession of invalid and misapplied nomenclature involving eight generic names: *Epidendrum* L., *Encyclia* Hook., *Dichaea* Lindl., *Prosthechea* Knowles & Westc., *Epithecia* Knowles & Westc., *Hormidium* Lindl. ex Heynhold, *Anacheilium* Hoffmanns., and *Microepidendrum* Brieger. This classical case of nomenclatural confusion has resulted in a problematic taxonomic classification of the genus *Encyclia*. Soon after W.J. Hooker established the genus, J. Lindley combined it with *Epidendrum*. In 1881, G. Bentham subdivided the section *Encyclium* into three series: *Dinema*, *Prosthechea*, and *Encyclia*. Schlechter revived usage of *Encyclia* at the generic level in 1914. In 1961, R. Dressler redefined *Encyclia*, expanding on Bentham's concepts. No sooner did Dressler assemble the genus than other taxonomists began to disassemble it. In 1960, F.G. Brieger started moving taxa into *Hormidium*. Pabst refined Brieger's concepts in 1981 and moved additional taxa. In 1997, W.E. Higgins resurrected the genus *Prosthechea* for *Encyclia* subgenus *Osmophytum*. In 2000, Higgins used nuclear and plastid DNA sequence data to estimate the phylogeny of *Encyclia* sensu Dressler. The Internal Transcribed Spacer (nrITS), *trnL-F*, and *matK* regions were sequenced. DNA sequence plus indel matrix was analysed with a successively weighted parsimony analysis. Bootstrap indices were used to estimate confidence in tree topology. As a result of this work, the genus *Encyclia* sensu Dressler has been divided into six genera: *Encyclia*, *Euchile*, *Dinema*, *Oestlundia*, *Prosthechea*, and *Microepidendrum*.

INTRODUCTION

Phylogenetic systematics is based on the evolutionary concept that natural groups have a common ancestor and all descendents of that ancestor are members of the natural group. These natural groups, called monophyletic groups or clades, are produced using phylogenetic analysis based on the principle of parsimony or Ockham's razor. This scientific principle holds that the simplest explanation of observed phenomena is most likely correct. The clades produced by phylogenetic analysis are based on shared derived (evolved) characteristics of the organisms under study. Thus phylogenetic analysis produces the groups that are the basis of a classification system.

Taxonomy is the application of naming groups in a hierarchical system, i.e., species are grouped into genera, into subtribes, etc. The International Code of Botanical Nomenclature governs the naming of these clades. This code addresses issues of name priorities, valid publication, conservation of names, etc. These regulations, however, do not address the issues of

species or generic level concepts. With biological concepts under constant discussion in the scientific community, molecular systematics is a valuable tool in defining the clades for taxonomic applications. Plant morphology, however, is most helpful when applying generic level concepts to produce a useful classification system. The purpose of a classification system is to provide a tool for plant identification. That tool should be "user friendly" and simple to apply based on visible characters of the plants. A classification system should allow the user to predict the placement of an unknown organism, based on the characteristics of known species.

TAXONOMIC HISTORY

Since Hooker (1828) described *Encyclia*, many species have been moved into and out of the genus by various taxonomists. Because members of the following eight genera have been included in *Encyclia* at different times, their taxonomic histories are discussed below.

Artorima

This genus was described by Dressler and Pollard (1971) for *Encyclia erubescens* (Lindl.) Schltr. (1914b), because the retrose, hook-like callus does not fit into any known genus. Brieger (1977a) invalidly transferred *Epidendrum kermesinum* Lindl. to *Artorima*. Ortiz (1995) then inexplicably transferred that species to *Encyclia kermesina* (Lindl.) Ortiz.

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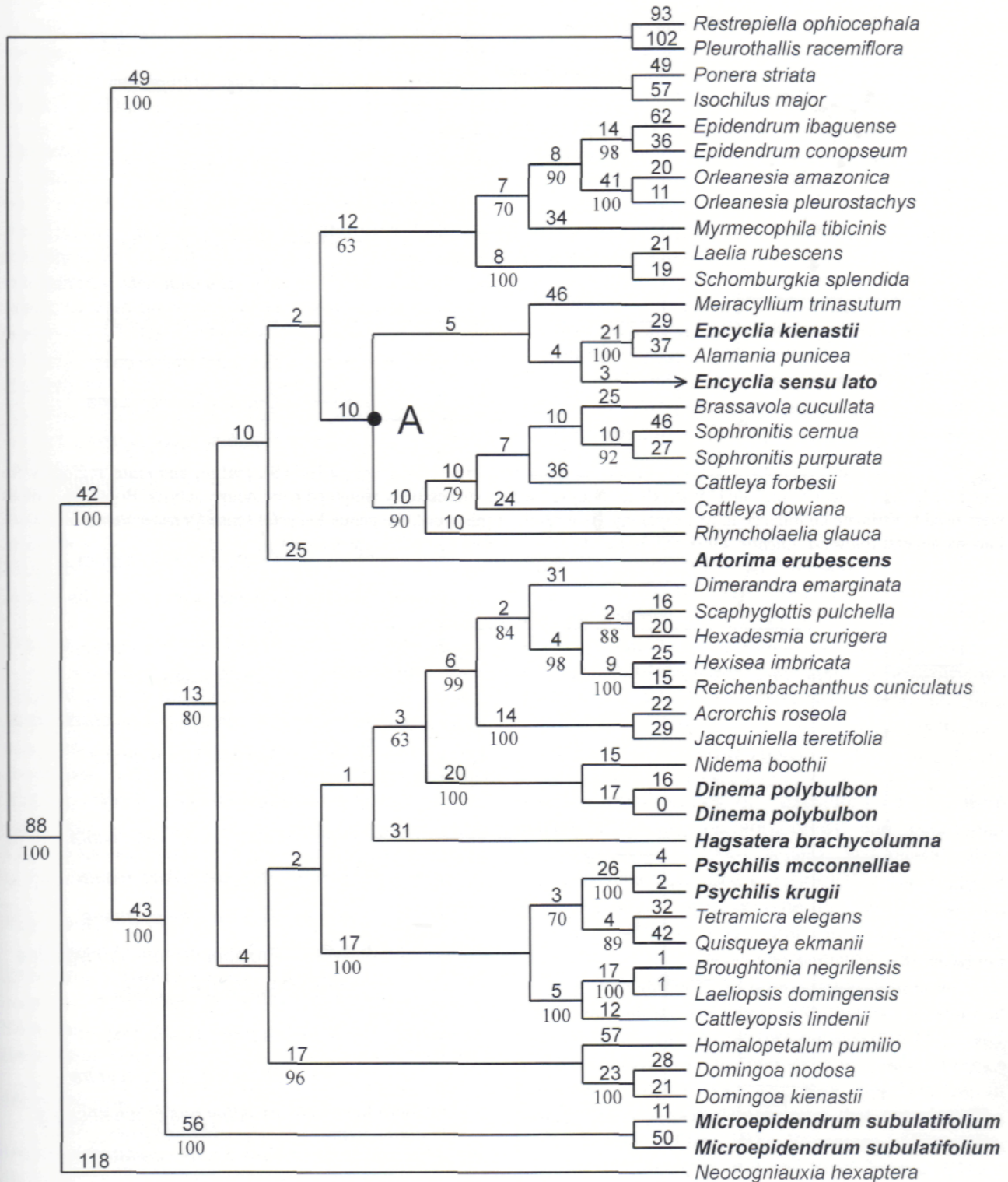


Fig. 1. Phylogenetic tree of Laeliinae based on a combined DNA matrix. Taxa in bold = former members of *Encyclia* s.l. Fitch branch lengths are above the line, and weighted bootstrap indices below. The node that collapses in the strict consensus tree is marked with a dot forming a trichotomy at point A. The *Encyclia* s.l. clade continues in Fig. 2.

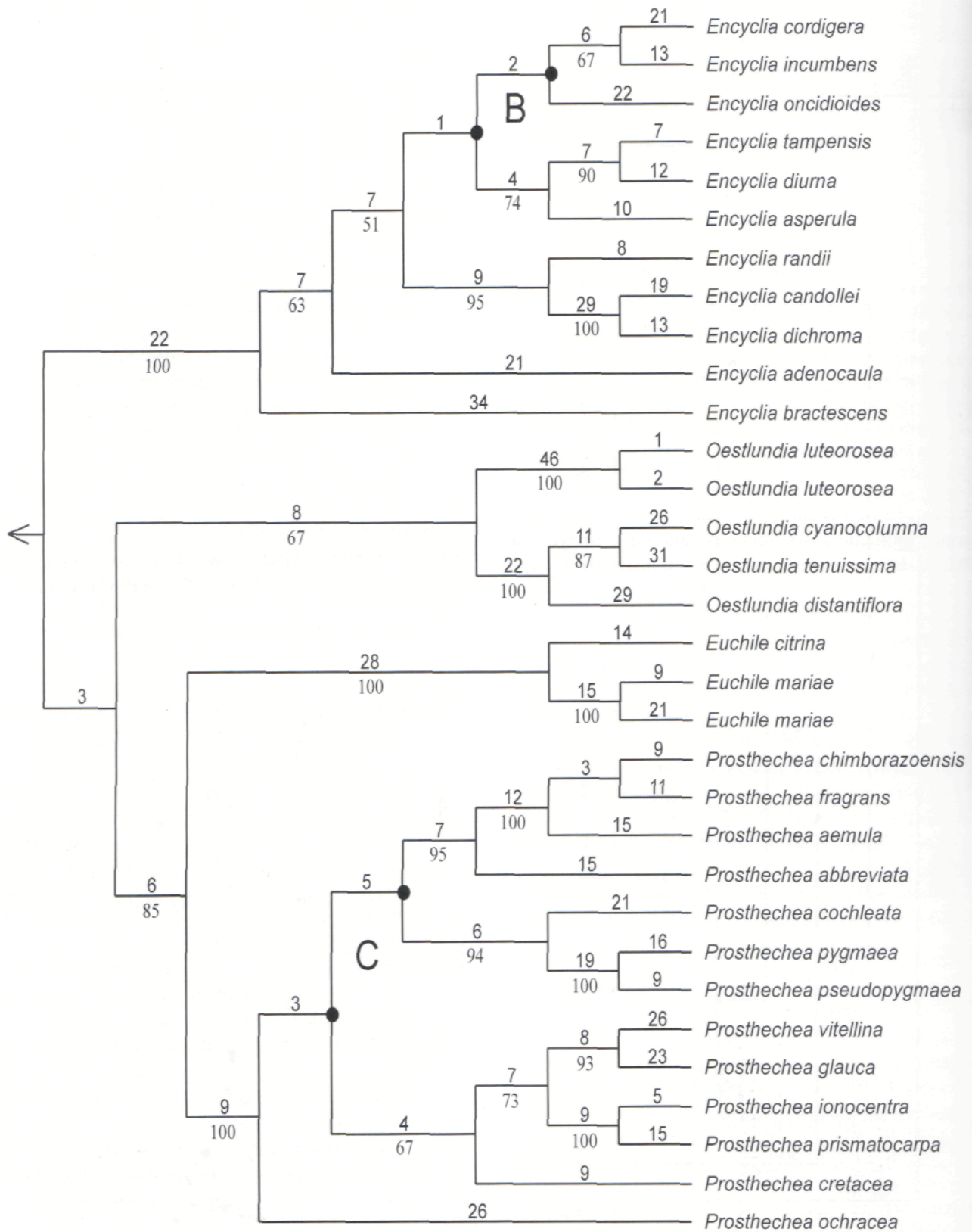


Fig. 2. Phylogenetic tree of *Encyclia* s.l. based on a combined DNA matrix. Fitch branch lengths are above the line, and weighted bootstrap indices below. The nodes that collapse in the strict consensus tree are marked with a dot forming polytomies at points B and C. This tree connects to Laeliinae (Fig. 1) at the arrowhead.

Dinema

The genus *Dinema* was established when Lindley (1831) made the combination *Dinema polybulbon* (Sw.) Lindl. This taxon had originally been described as *Epidendrum polybulbon* by Swartz (1788). Dressler (1961) transferred the taxon to *Encyclia*. *Encyclia* subgenus *Dinema* (Lindley) Dressler & Pollard was established because the taxon did not fit into the other subgenera (Dressler and Pollard, 1974).

Encyclia

Hooker (1828) described the genus *Encyclia* based on *E. viridiflora*. Subsequently, Lindley sank the genus into *Epidendrum* subgenus *Encyclium* in 1853. *Encyclia* was unused until Schlechter (1914a) revived it. Other taxonomists then started placing various taxa in the genus. Lemée (1955) inexplicably transferred five taxa from *Epidendrum* subgenus *Aulizeum* Lindl. to *Encyclia*, thereby enlarging the circumscription of *Encyclia* by Schlechter. Dressler (1961) circumscribed *Encyclia* describing two sections, *Encyclia* section *Encyclia* and *Encyclia* section *Osmophytum*. Subsequently, Dressler and Pollard (1971) revised the genus to include six sections and three subgenera. Pabst, Moutinho and Pinto (1981) transferred the taxa in *Encyclia* section *Hormidium* Dressler to *Hormidium*. They then transferred part of the taxa in *Encyclia* section *Osmophytum* to *Anacheilium*.

Euchile

At various times, taxa in this group have been assigned to *Sobralia*, *Cattleya*, *Epidendrum*, *Encyclia*, *Hormidium*, or *Prosthechea*. *Encyclia* section *Euchile* was described by Dressler and Pollard (1971) for anomalous taxa in *Encyclia* subgenus *Osmophytum*. Withner (1998) raised the sectional name to generic status because of the atypical pattern of epidermal cells. The two species in this group were considered members of *Prosthechea* by Higgins (1997) in the past.

Hagsatera

Roberto González (1974) described this genus for *Epidendrum brachycolumna* L.O. Williams that had been placed into *Encyclia* by Dressler (1961). This was based on a short column and eight pollinia atypical of *Encyclia* or *Epidendrum*.

Microepidendrum

When Brieger (1977b) published the genus *Microepidendrum*, he failed to provide a Latin diagnosis or designate a type species invalidating his combination *Microepidendrum subulatifolium* (A. Rich. & Gal.) Brieger. Dressler classified this species in *Encyclia* section *Leptophyllum*.

Oestlundia

The genus *Oestlundia* W.E. Higgins was established for four members of *Encyclia* subgenus *Encyclia* section *Leptophyllum* Dressler & G.E. Pollard

(Higgins, 2001). The name *Oestlundia* commemorates Karl Erik Magnus Östlund (1875–1938), who collected the type specimen for this genus.

Prosthechea

Knowles and Westcott (1838) first published *Prosthechea* to describe the species *P. glauca*. In the following year, however, they changed the generic name to *Epithecia*, because they felt that *Prosthechea* was too similar to another unspecified generic name (Knowles and Westcott, 1839). This new name was superfluous since *Prosthechea* had been validly published. *Prosthechea* has been resurrected (Higgins, 1997, 1999), and species in *Encyclia* subgenus *Osmophytum* renamed *Prosthechea*.

Psychilis

The genus *Psychilis* was described by Rafinesque (1838) based on *Psychilis amena*, but the generic name was ignored, and most members of *Psychilis* have been considered *Encyclia*. Schlechter (1914a) transferred *Epidendrum atropurpureum* Willd.; Britton and Wilson (1930) transferred *Epidendrum krugii* Bello; Schrenk (1977) transferred *Epidendrum bifidum* Aubl.; Beckner (1970) transferred *Epidendrum olivaceum* Cogn. and *Epidendrum truncatum* Cogn.; Dod (1983) described *Encyclia vernicosa* and transferred *Epidendrum cogniauxii* L.O. Williams, *Epidendrum buchii* Cogn., and *Epidendrum domingense* Cogn.; and Ackerman (1987) transferred *Epidendrum kraenzlinii* Bello to *Encyclia*. Saulea (1988), however, reestablished the genus and transferred the above to *Psychilis*.

DISCUSSION

The relationships of “*Encyclia*” species were examined using holomorphology and parsimony analysis (Higgins, 2000). Nuclear and plastid DNA sequence data were used to estimate the phylogeny of *Encyclia* sensu Dressler. The Internal Transcribed Spacer (nrITS), *trnL-F*, and *matK* regions were sequenced. The DNA sequence matrix was analysed with a successively weighted parsimony analysis. Bootstrap indices were used to estimate confidence in tree topology. The phylogenies presented in Fig. 1 and 2 were produced by this three-gene molecular study of Laeliinae (Higgins, van den Berg and Whitten, in press). Fig. 1 clearly demonstrates that *Artorima* (Fig. 3A), *Dinema* (Fig. 3B), *Hagsatera*, (Fig. 4D), *Microepidendrum* (Fig. 3C), and *Psychilis* (Fig. 3D) are not members of the same clade as *Encyclia*.

The placement of *Encyclia kienastii* (Fig. 4A) as the sister to *Alamania punicea* highlights the need for additional study of this clade. In Fig. 2, *Encyclia* is sister to the clade containing *Oestlundia*, *Euchile*, and *Prosthechea*. The taxonomic decision to split this sister clade from *Encyclia* is based on the morphological characteristics of the plants and on the principle of

Table 1. Morphological characteristics distinguishing major genera in the *Encyclia* sensu lato clade.

Characteristic	<i>Encyclia</i> sensu stricto	<i>Prosthechea</i>	<i>Euchile</i>	<i>Oestlundia</i>
Pseudobulbs	Usually ovoid or conic-ovoid	Fusiform, usually flattened	Conic-ovoid or fusiform-ovoid	Ovoid to conic-ovoid
Leaves	Thick	Usually thin	Thin	Thin
Glycoside crystals	Absent	Usually present	Absent	Absent
Inflorescence	Scape without spathe	Scape or sessile with prominent spathe	Scape without spathe	Scape without spathe
Flower	Resupinate	Usually non-resupinate	Resupinate	Resupinate
Labellum callus	2 fleshy ridges	Usually a thick pad	Laminar ridges	Papillae
Labellum adnate	Usually at base	Half of column	At base	At base
Column	Often winged	Never winged	Not winged	Not winged
Column mid-tooth	Short, usually broadly deltoid	Large, narrowly deltoid, ligulate, or subflabellate	Large, truncate, subequal to lateral teeth	Short, rounded, shorter than lateral teeth
Mid-tooth appendage	Absent	Fleshy, knob-like, obtuse or truncate	Absent	Absent
Mid-tooth to anther	Appressed	Not appressed	Not appressed	Appressed
Column sinuses	Broad shallow	Deep usually acute	Deep	Shallow
Lateral teeth	Short	Stout	Stout	Wing-like
Rostellum	Vertical	Vertical	Vertical	Horizontal
Seed capsule	Fusiform 3-winged or sharply 3-angled	Weakly triangular	Fusiform	
Capsule suture	Strap absent	Covered by strap of tissue	Strap absent	Strap absent

having a simple, user-friendly, and predictive classification. This sister clade forms three cohesive groups, *Oestlundia*, *Euchile*, and *Prosthechea*. Although the author previously included *Euchile* in *Prosthechea*, several good characters distinguish it from *Prosthechea*. *Euchile* flowers are not filled with glycoside crystals; the fragrance composition is different (Kaiser, 1993); the mid-tooth is not ligulate; and leaf epidermal cells have an atypical pattern (Withner, 1998).

A good classification should have maximum general utility, i.e. easy to use, concise, predictive, an aid to memory, and stable (Gilmour, 1940). Current genera are built on the Linnaean principle of reproductive characters serving as the major source of generic-level characters (Judd *et al.*, 1999). Although *Encyclia s.l.* could be recognized at the generic level, recognition of *Encyclia s.s.*, *Euchile*, *Prosthechea*, and *Oestlundia* at the generic level is more predictive, based on the morphological characteristics. *Encyclia* (Fig. 4B) has a two fleshy-ridged callus on the lip, the column has a small mid-tooth appressing the anthercap and two short large deltoid lateral teeth, and the column is often winged. *Euchile* (Fig. 4C) has glaucous leaves, a lip that encircles the column, a nectary at the base of the column, and three large truncate teeth on the column. *Prosthechea* (Fig. 3E) has fusiform pseudobulbs often flattened, a prominent spathe, a thick-pad callus, lip adnate one-half of column, three large knob-like teeth on column, ligulate mid-tooth, and a 3-winged/angled seed capsule with a strap covering the suture (Higgins, 1999). *Oestlundia* (Fig. 3F) has a small mid-tooth that appresses the anther and two large wing-like lateral teeth, the rostellum in a horizontal position between the lateral teeth, and small pseudobulbs with grass-like leaves. A summary of the morphological characters defining these genera is found in Table 1. An *Encyclia sensu stricto* classification is preferred to *Encyclia sensu lato* because of morphological differences and DNA phylogeny.

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Figures not given here are presented in Plates 16–17 (Page 371–372).

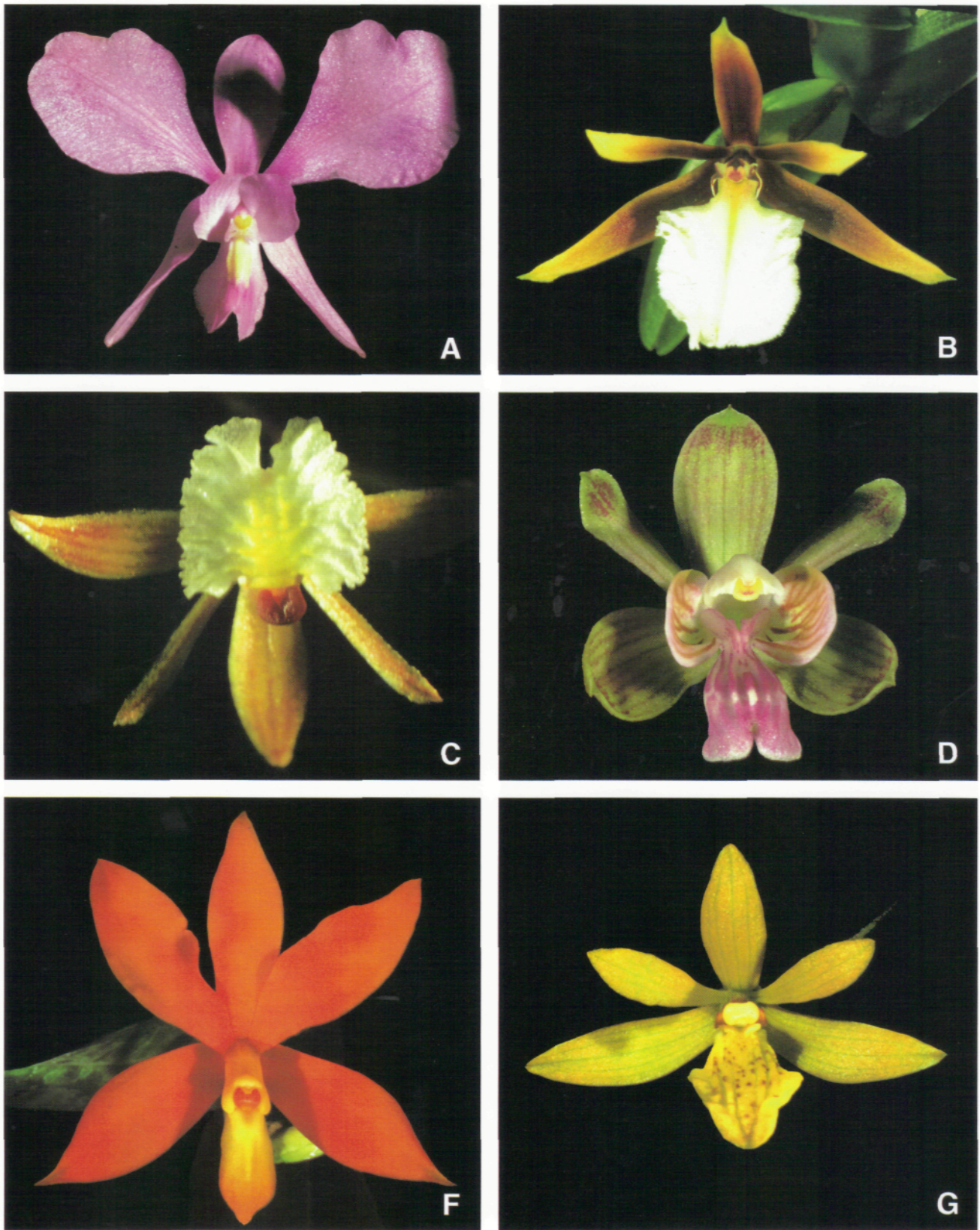


Fig. 3. A. *Artorima erubescens* (Photo by E.W. Greenwood); B. *Dinema polybulbon*; C. *Microepidendrum subulatifolium*; D. *Psychilis krugii*; E. *Prosthechea vitellina*; F. *Oestlundia tenuissima*.

For full text, refer to page 134–140.

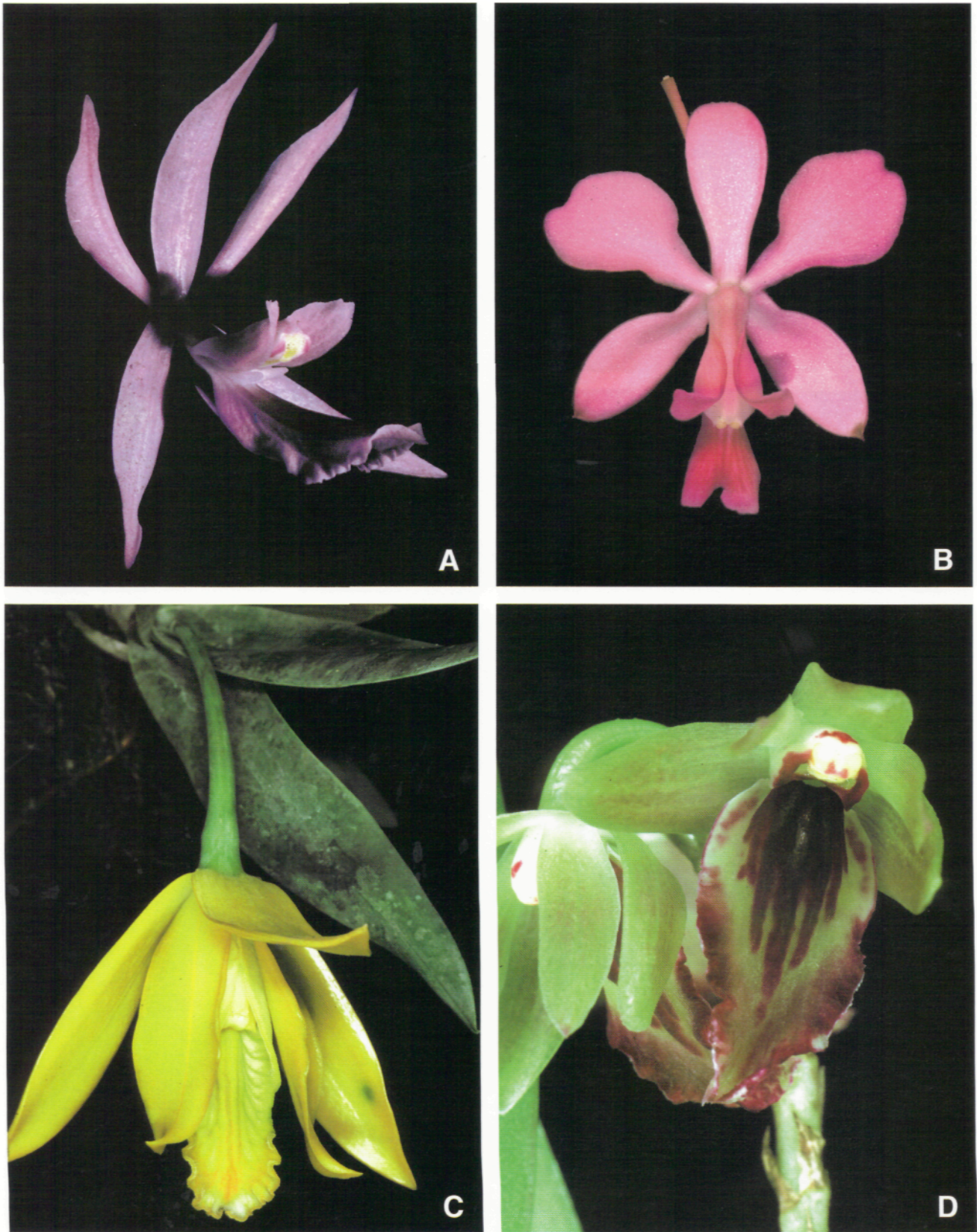


Fig. 4. A. *Encyclia kienastii* (Photo by Raymond McCullough); B. *Encyclia dichroma*; C. *Euchile citrina* (Photo by Mark Whitten); D. *Hagsatera brachycolumna* (Photo by Gerardus B. Staal).

For full text, refer to page 134–140.