



## Checklist of mycoheterotrophic species of the genus *Exacum* (Gentianaceae) and new species, *E. zygomorpha*, from northern Vietnam

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### Abstract

The paper provides a key for identification and a checklist of mycoheterotrophic species of the genus *Exacum*, representing a well-defined group of achlorophyllous members of Gentianaceae regarded sometimes in the limits of a separate genus *Cotylanthera*. One novel species, *E. zygomorpha*, discovered in northern Vietnam, is described and illustrated as new for science. Among other features the discovered species strikingly differs from its congeners in having distinctly zygomorphic flowers.

### Introduction

The group of mycoheterotrophic, achlorophyllous species of the genus *Exacum* L. (1753: 112) presently includes 5 species from tropical Asia from Nepal and Bhutan through China, Indochina and Indonesia to the Philippines and New Guinea. This group recognized in the past as the genus *Cotylanthera* (Blume 1826), forms a well-defined group of mycoheterotrophic achlorophyllous members of the Gentianaceae, which since their discovery (Blume 1826) were traditionally regarded in a separate genus (Gray 1869, Clarke 1883, Gilg 1895, Lace 1914, Smith *et al.* 1921, Hara 1975). The most recent taxonomic treatment (Hara 1975) summarized the specimens available in herbaria and provided adequate data about morphology, diagnostic features and distribution of the 4 species of the group recognized at that time. Important new details on the distribution of some mycoheterotrophic species were reported in the following publications: Ho Ting-nung & Pringle (1995), Hul (2003) and Biswal *et al.* (2011). One of the first monographers of the Gentianaceae proposed tentative inclusion of *Cotylanthera* as a section within the widespread and variable genus, *Exacum* Linnaeus (1753: 112) (Baillon 1891). More than a century later this idea received some support from molecular investigations that suggested mycoheterotrophic *Cotylanthera* species are nested inside *Exacum* (Yuan *et al.* 2003, Merckx *et al.* 2013). In response, species of *Cotylanthera* were transferred into *Exacum* with necessary nomenclatural name changes (Klackenberg 2006). At the same time, molecular studies revealed specific characters of *Cotylanthera* species that make correct phylogenetic analysis fairly problematic (Yuan *et al.* 2005). Because of these findings the present taxonomic position of the genus remains uncertain. It seems reasonable to recognize this specific group of species as a distinct separate group based on the possible evolution of *Exacum*-like ancestors produced through paraphyletic derivation and through the evolution of the mycoheterotrophic mode of life and degradation of its photosynthetic system. The achlorophyllous habit in mycoheterotrophic species here strongly correlates with the formation of slender dwarf stems, tuberous roots (lacking root hairs) and deep reduction of leaves as happens in many similar mycoheterotrophic evolutionary lines of flowering plants (Leake 1994). It is notable that all members of the genus are very rare unattractive plants easily overlooked in botanical surveys and poorly represented in world herbarium collections. This explains why there are extensive and essential gaps in our knowledge about the genus. In this connection the new species described and illustrated here represents a significant missing link in global understanding of the evolution of the genus, its specialization, diversity and distribution. The paper also provides a key for identification and a checklist of all currently known mycoheterotrophic species of *Exacum* summarized from all presently available data.

## Taxonomic treatment

*Exacum* L. (1753: 112), pro mycoheterotroph. sp. parte.

*Cotylanthera* Blume (1826: 707).

*Eophylon* Gray (1869: 22).

5 species in Nepal, Bhutan, NE. India, Myanmar, SW. China, Thailand, Laos, Vietnam, Philippines, Indonesia and New Guinea.

## Key to species

1. Anthers subsessile with distinctly extended connective at the apex ..... 1. *E. loheri*  
– Anthers with distinct filament without extended connective at the apex ..... 2
2. Corolla 3–10 mm long; anther less than 3 mm long, oblong to narrowly oblong, obtuse or indistinctly cordate at the base; style 3–5 mm long ..... 3  
– Corolla 10–14 mm long; anther 3.5–5.5 mm long, sagittate, deeply cordate at the base; style 6–8 mm long ..... 4
3. Stem simple; flowers 3–6 mm long; petals obtuse; filaments longer than the anther, 1.5–2.5 mm long; anthers oblong, 1.2–1.8 mm long ..... 2. *E. caerulea*  
– Stem usually branched; flowers 6–10 mm long; petals apiculate; filaments shorter than the anther, rarely as long as anther; anthers narrowly oblong to oblong, 1.8–3 mm long ..... 3. *E. tenuis*
4. Stem usually simple; inner and outer sepals subsimilar; flowers widely opening, pale mauve to blue, petals spreading, obtuse; stamens straight or slightly curved on one side; filaments 2–3 mm long, shorter than anther; anthers sagittate, dehiscent by a small apical pore; style straight or slightly curved; stigma capitate; ovary 2-celled ..... 4. *E. paucisquama*  
– Stem usually branched; inner sepals distinctly shorter and broader than outer sepals; flowers not widely opening, pure white, petals connivent, curved to one side, blunt or round at the apex; stamens distinctly curved to one side; filaments 3.5–4 mm long, as long as anther; anthers narrowly sagittate, often abortive indehiscent, or dehiscent by a small apical pore; style distinctly curved on one side; stigma truncate discoid; ovary 1-celled ..... 5. *E. zygomorpha*

1. *Exacum loheri* (Hara) Klackenberg (2006: 478).

Synonym: *Cotylanthera loheri* Hara (1975: 327) figs. 4f–i, 5.

**Type:**—PHILIPPINES. Luzon central: Montalban, October 26, 1895, *A.Loher 5189* (holotype K!).

**Distribution:**—Philippines.

2. *Exacum nanum* Klackenberg (2006: 478).

Synonym: *Cotylanthera caerulea* Lace (1914: 154).

**Type:**—MYANMAR. Upper Burma: Maymyo, 1050 m, August 1912, *J.H.Lace 5898* (holotype K!, isotype E).

**Distribution:**—NE. India (Assam), Nepal, Myanmar, Thailand.

3. *Exacum tenue* (Blume) Klackenberg (2006: 478).

Synonyms: *Cotylanthera tenuis* Blume (1825: 708); *Eophylon lobbii* Gray (1869: 23); *E. tenellum* Gray (1869: 23); *Cotylanthera tenella* (Gray) Gilg in Engler & Prantl (1895: 64).

**Type:**—JAVA. Crescit: in umbrosis montis Menara (BO, L?).

**Distribution:**—E. India (Odisha), Philippines, Indonesia (Java, Sumatra, Kalimantan, Sulawesi), New Guinea.

4. *Exacum paucisquamum* (Clarke) Klackenberg (2006: 478).

Synonyms: *Cotylanthera paucisquama* Clarke (1883: 94); *Cotylanthera yunnanensis* Smith (1921: 158).

**Type:**—NE. INDIA. Sikkim; alt. 6000 ft., July 1875, *G.King 2163* (holotype CAL, isotype K).

**Distribution:**—Bhutan, NE. India (Sikkim, West Bengal), SW. China (Sichuan, Tibet, Yunnan), NW. Vietnam (Lao Cai).

5. *Exacum zygomorpha* Aver. & K.S.Nguyen, *sp. nov.* Figs 1–3.

*Small achlorophyllous herb with erect, slender, branched stem; leaves, opposite, scale-like; flowers hardly opening, white, asymmetric; calyx decussate, bisymmetric, 1–1.2 cm across; corolla of 4 petals, 1–1.2 cm long, zygomorphic; petals narrowly oblong, 2.5–3 mm wide, joined at the base; androecium slightly zygomorphic, one-side turned; anthers yellow, 4 × 1 mm long; ovary of 2 carpels, 1-locular, almost globular 1.5 mm in diam.; style thread-like, 8–8.5 mm long; stigma entire.*

**Type:**—VIETNAM. Nghe An Prov., Ky Son Distr., Nam Can Municipality, Tham Hin village, eastern slopes of Phu Xai Lai Leng Mountain. Primary humid broad-leaved forest on steep mountain slopes composed of sandstone and gray shale at elev. 2000–2300 m around point 19°12'13.57"N 104°11'35.66"E. October 24, 2013, *L.Averyanov, N.T.Hiep, N.S.Khang, L.M.Tuan, N.A.Trang & L.H.Dan, CPC 6183* (holotype LE!, isotype Herbarium of the Center for Plant Conservation, Hanoi).

Small achlorophyllous pure white mycoheterotrophic herb 5–8 cm tall. Roots numerous, clustering on short underground plagiotropic rhizome, fleshy, finely longitudinally wrinkled, separated by narrowing restrictions into fusiform portions 0.5–1 cm long, 1–2 mm in diam. Stem erect, slender, glabrous, branched like a simple cyme into 3 floriferous branches at the middle or in its lower portion, terete to indistinctly quadrangular, 1–2 mm in diam., indistinctly ridged, slightly swollen below nodes. Leaves numerous, opposite, scale-like, triangular, obtuse to acute, (1–)1.5–3 × 1–1.5 mm, internodes (3–)5–15(–20) mm long. Flowers terminal, solitary, 4-merous, asymmetric (zygomorphic-like), pure white, anthers dull light yellow. Calyx campanulate, slightly bisymmetric (having biaxial symmetry), 1–1.2 cm across, consist of 4 paired opposite, decussate, fleshy, spreading scales with distinct midvein, fused at the base; two outer scales narrowly triangular, acute, 5–6 × 2.5–3 mm; inner scales smaller and broader, shortly attenuate, with membranous, finely irregularly incised margin. Corolla of 4 petals, 10–12 mm long, zygomorphic; petals erect, connivent and obliquely one side turned, narrowly oblong, entire, 2.5–3 mm wide with 3 nerves, blunt or round at apex, joined on 2 mm from the base, forming globular tube 2 mm in diam., embracing ovary. Androecium slightly zygomorphic, stamens inserted at throat of corolla tube below sinus between petals, 8 mm long, shorter than petals (on 1–2 mm), all one-side turned; filaments subterete, 3.5–4 mm long; anthers 4 mm long, slightly curved, introrse, dorsifixed, sagittate, 1 mm wide at the base, narrowing to the apex, incompletely 2-locular, dehiscing by apical pores or abortive, indehiscent. Ovary of 2 carpels, 1-locular, broadly ovoid to globular 1.5 mm in diam., attenuate at the apex into distinctly bent, terete, thread-like style 8–8.5 mm long; stigma terminal, small, entire, truncate, discoid. Placentation free central with massive 4-lobed column bearing many ovules, divided to the apex into 4 short narrow sterile stalks. Fruits not seen.

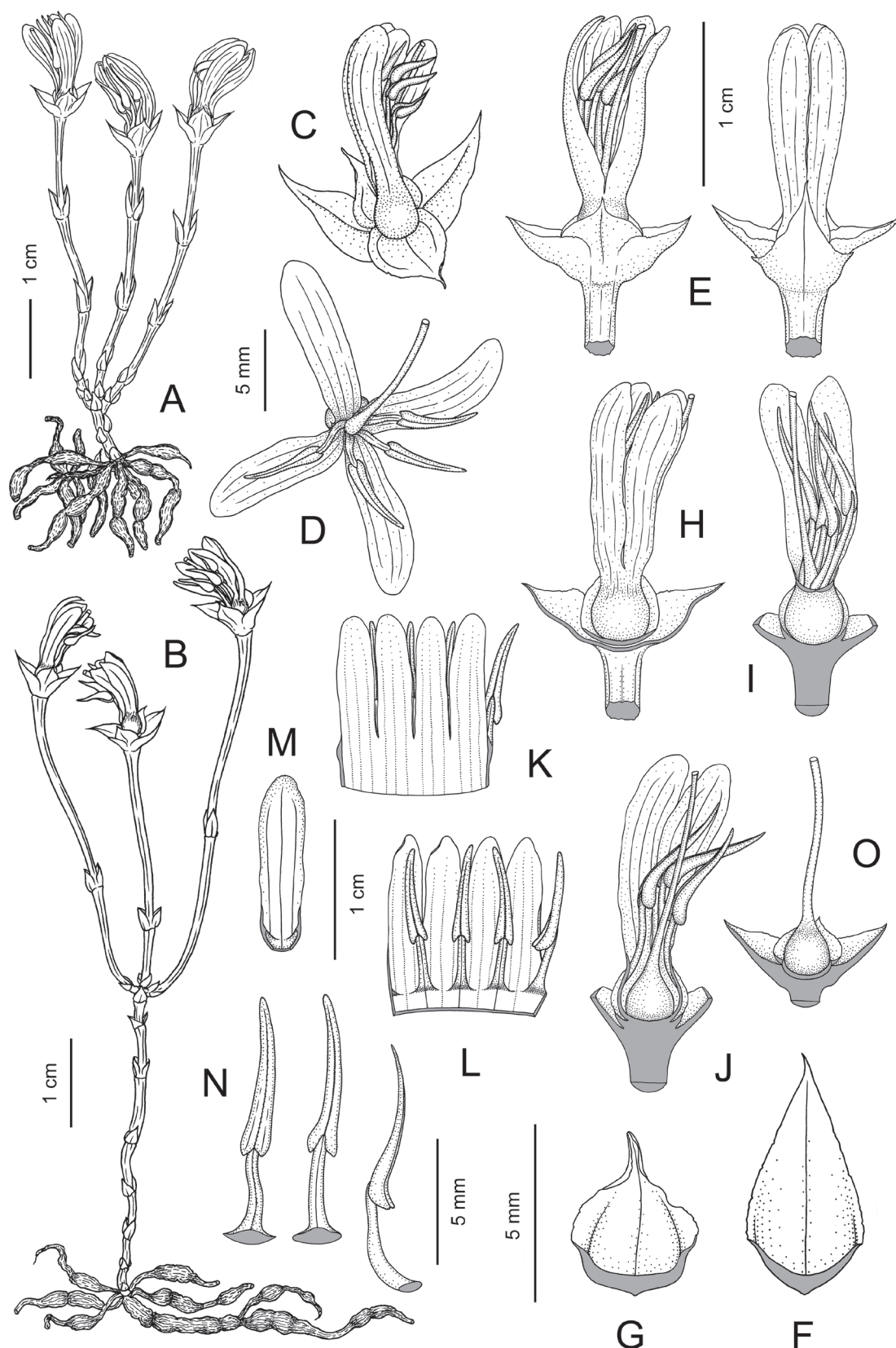
**Etymology:**—Species name refers to distinct zygomorph-like asymmetry of its flowers.

**Distribution:**—Vietnam (Nghe An). Only one locality in Phu Xai Lai Leng Mountain on the border of the provinces Xiangkhouang (Laos) and Nghe An (Vietnam).

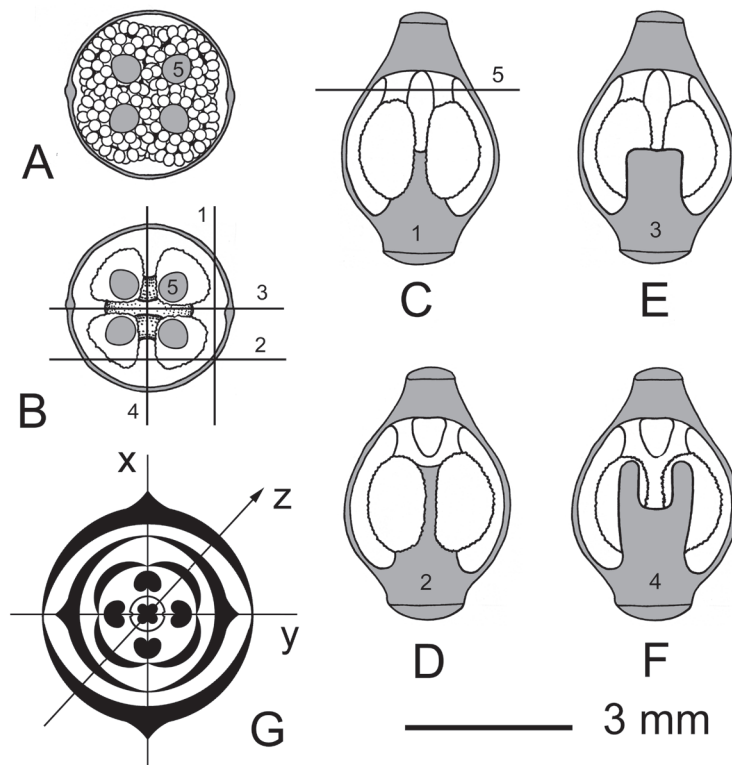
**Ecology:**—Primary humid shady broad-leaved and mixed forests (with *Cunninghamia konishii*) on soils rich in humus derived from sandstone and shaly rocks at elev. 2000–2300 m, usually along ridge edges. It flowers from October–November. Very rare.

**Notes:**—New species has obviously near-affinities to *Exacum paucisquama* but it differs in its branching stem, bisymmetric (having biaxial symmetry) decussate calyx, flowers not opening widely, pure white, distinctly asymmetric flowers and a 1-celled ovary. Connivent curved petals, hanging over anthers, hardly opening, an unattractive corolla and abortive anthers lacking pollen observed in the new species as well as the development of the ovary and numerous ovules suggests the seed formation may be by apomixis without pollination. The new taxon exhibits a pronounced trend in asymmetric floral formation well-expressed in other *Exacum* species. Asymmetry of the flower in the new species is a result of secund bending of petals and stamens (of basically an actinomorphic corolla and androecium) on one side along the bisectrix of the perpendicular axes of the bisymmetric calyx (fig. 1I, J, 2G). The one-celled ovary of *E. zygomorpha* is unique in the genus. The ovary has free central placentation with 4-lobed, massive, column-like placenta divided to the apex into 4 short narrow sterile stalks (fig. 2A–F).

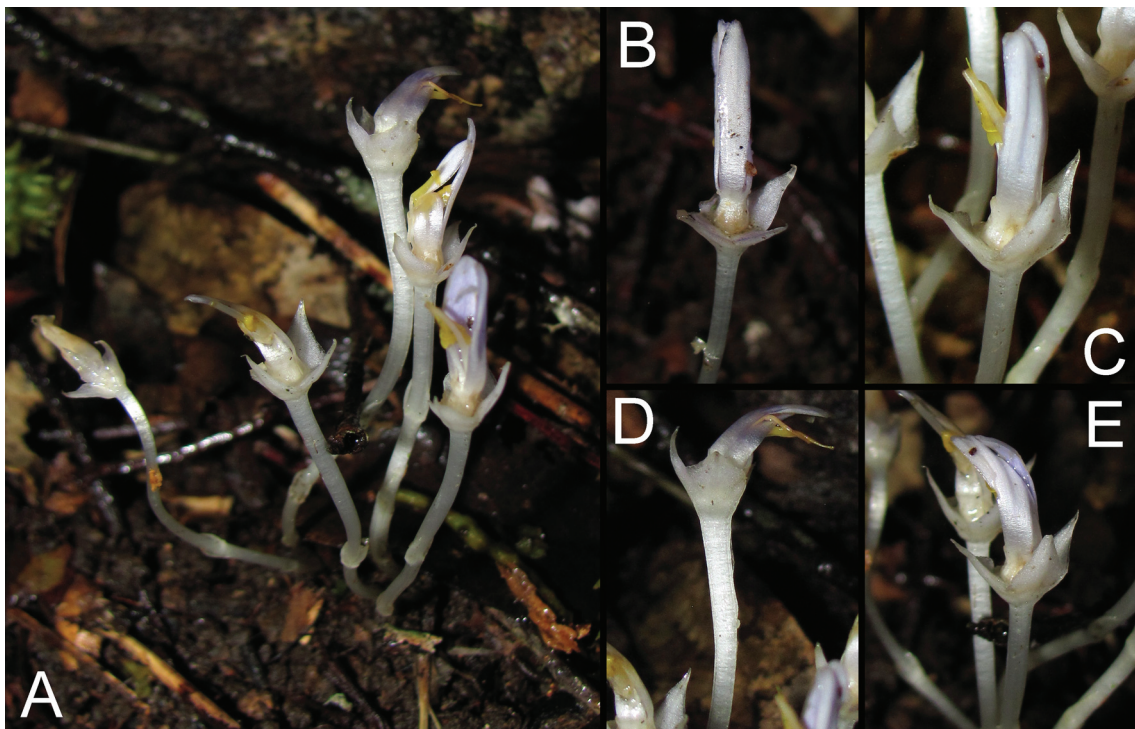
A blue-flowered specimen from Vietnam collected within the Hoang Lien Son Range near Sapa town in Lao Cai province (*Poilane 12648*) are certainly very similar to *E. paucisquama* while distinctly differing in having a branching stem, as well as apiculate petals and therefore probably represent a separate undescribed species. This taxon needs additional collections and observations from Hoang Lien Son mountain area to better understand this unusual plant.



**FIGURE 1.** A, B: Flowering plants. C: Opened flower, half side view. D: Flower with artificially recurved and flattened petals and stamens. E: Flowers, side views. F: Outer sepal. G: Inner sepal. H: Flower, side view with sagittal section of the calyx. I: Flowers, side view with sagittal section of the calyx and two petals removed from place of their junction into tube. J: Flower, side view, sagittal section. K: Removed and flattened petals, view from outside. L: Removed and flattened petals, view from inside. M: Flattened sepal, adaxial surface. N: Stamens, abaxial, adaxial and side views. O: Ovary with removed corolla and sagittal section of the calyx. All drawn from the type—CPC 6183 by L.Averyanov and T.Maisak.



**FIGURE 2.** A–F: Ovary sections: A—transversal section of ovary along line 5 (designated on fig C); B—transversal section of ovary along line 5 (designated on fig. C) with ovules removed; C—longitudinal tangential ovary section along line 1 (designated on fig. B); D—longitudinal tangential ovary section along line 2 (designated on fig. B); E—sagittal radial ovary section along line 3 (designated on fig. B); F—sagittal radial ovary section along line 4 (designated on fig. B). G: Floral diagram; x and y—symmetry axes of bisymmetric (biaxial) decussate calyx; z—approximate symmetry axis and bending direction of zygomorphic corolla, stamens and style. All drawn from the type—*CPC 6183* by L.Averyanov and T.Maisak.



**FIGURE 3.** A: Flowering plants in native habitat. B: Flower bud at the beginning of anthesis. C–E: open flowers, views from different sides. All photos from the type—*CPC 6183* by Khang Sinh Nguyen, correction and design by L.Averyanov.

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