Development of Laminar Expansion in *Cephalomanes meifolium* (Hymenophyllaceae)

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The evolution of *Cephalomanes meifolium* is discussed based on the developmental process of the ultimate segments, a key character in this species group, observed with living plants. It is suggested that the particular morphology of the ultimate segments of *Cephalomanes meifolium* may have evolved through special reduction of their surface.

**Key words:** *Cephalomanes meifolium*, developmental stage, evolution, Hymenophyllaceae, laminar expansion, ultimate segments.

**Introduction**

The filmy fern genus *Macroglena* sensu Copeland (now treated as a subgenus under *Cephalomanes* by Iwatsuki) was critically discussed by Iwatsuki (1981). In that revision, *Cephalomanes meifolium* and *C. setaceum* were considered to be specialized because of their setaceous ultimate frond segments. Other characters suggested that the morphological similarity between the adults of those two species was a consequence of parallel evolution. Therefore, the two species were interpreted as members of different, independent series: (1) *Trichomanes meifolium*–*T. gemmatum*–*T. clathratum* and (2) *T. setaceum*–*T. kalimantanense*–*T. obscurum*.

Iwatsuki (1962) compared the venation pattern of sporophyte fronds of *Stegnogramma griffithii* during their development. Based on those comparative observations, he was able to trace the sagenoid venation of this species throughout its life history and concluded that *S. griffithii* does not display goniopteroid venation during any part of its ontogeny. Such ontogenic comparisons can provide good evidence for evaluating the usefulness of phenetic characters in determining phylogenetic relationships among the species.

In the course of a botanical excursion in Malaysia in 1998, Jaman and Iwatsuki collected a number of juvenile plants of *Cephalomanes meifolium* on Pine Trail on Frazer’s Hill. We used those plants to trace the developmental stages of the ultimate segments carefully from the first leaves to those in the adult stage. We noticed that the ultimate segments of the fronds in the early developmental stages in *C. meifolium* show a similar morphology in the arrangement of their laminar cells to those of the adult form.
of *C. gemmatum*. We suspect that the morphology of the ultimate segments of the fronds of the adult leaves of *C. meifolium* is specially induced, as inferred from the morphology of the juvenile stage.

In this short article, we describe the morphology of the ultimate segments of the fronds of *Cephalomanes meifolium* throughout their development and compare them with the morphology of the ultimate segments of the fronds of *C. gemmatum*.

**Materials and Methods**

Juvenile plants of *Cephalomanes meifolium* were collected on Pine Trail on Frazer's Hill, Pahang, Malaysia, at an elevation of about 1300 m, on 24 November, 1998. We then observed the fresh fronds, which ranged in development from the first fronds of the sporophytes to those of the adult plants, through their successive developmental stages (Fig. 1). The morphology of the ultimate segments was observed with particular reference to the influence of cellular arrangements on laminar construction. The ultimate segments of *C. gemmatum* were also carefully observed and compared with those of the juvenile forms of *C. meifolium*.

**Results and Discussion**

Fig. 1 is a photo of the fronds of *C. meifolium* at different developmental stages. The first and second juvenile fronds of *C. meifolium* produced by the prothallium were bifurcate, with the lobes composed of five or six rows of cells on each side of the midrib. The laminar cells were elongate-tetragonal or nearly tetragonal in surface view, and the segments and rachis were arranged in one plane, contrary to the cubic arrangement seen in the adult form (Figs. 1–A, 2, 3). Each of the third and fourth fronds has a few pinnately arranged lobes similar to those of the first and second fronds in both morphology and arrangement, although larger fronds generally showed non-unifacial (bifacial) arrangement of the lobes. In the fourth and subsequent fronds, the laminar expansion

![Fig. 1. Fronds of *Cephalomanes meifolium* at different developmental stages.](image)
Figs. 2-5. Fronds of Cephalomanes meifolium. Fig. 2. Juvenile fronds showing bifurcation, wings, and segments and rachis in one plane. Fig. 3. Segment with five or six rows of cells on each side of midrib; cells elongate-tetragonal or tetragonal in surface view. Fig. 4. Adult form with cubic frond. Fig. 5. Ultra segments. Wings reduced to setae with 0–2 rows of cells.
gradually varied in development: the rachis of the pinna and the higher order axes (e.g., rachis of secondary pinnae and midribs of ultimate segments) were arranged in various directions (Figs. 1-B, C, D), resulting in a cubic construction of the fronds. The laminar expansion of the lobes and ultimate segments was narrower in the later fronds, and those of the fourth and fifth fronds were reduced to only setaceous ultimate segments; the ultimate segments were sometimes bent, with a falcate outer portion (Figs. 1-C and D, 4-5). Some intermediate forms with three rows of cells were observed in the segments of the same fronds in individuals at the fourth and fifth frond stage.

Iwatsuki (1981) described the morphology of *C. meifolium* and related species in detail, although he observed the morphology of only adult plants at that time. He carefully noted the specialized dendroid construction of the fronds of *C. meifolium* to separate them taxonomically solely by this character. Iwatsuki (1981) also reported two evolutionary series in the morphological of the species of *Cephalomanes* are now under analysis using molecular systematic methods, and it has already been shown that *C. meifolium* is close to the other members referred to *Cephalomanes* s. l. (Ebihara et al. unpublished data).

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References