Juvenile Leaves and Leaf Ramification in *Phanerosorus major* (Matoniaceae)

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加藤雅啓・岩槻邦男：*Phanerosorus major*（マトニア科）の幼葉と分枝

*Phanerosorus* Copel. (1909) is a fern genus of two species that along with *Matonia* of one variable species constitutes the family Matoniaceae (Copeland, 1947). *Phanerosorus* differs greatly from *Matonia* in leaf morphology and also in habitat: *Phanerosorus* grows pendent from limestone cliffs, while *Matonia* is terrestrial with erect leaves in mossy, exposed mountain peaks or ridges. Its distribution is narrow and disjunct: *P. sarmentosus* (Bak.) Copel., type of the genus, is known only from Borneo (Sarawak) and *P. major* Diels has been collected in the islands Waigeo, Misool (*Pleyte 829*, BO), Seram and Aru (*Buwaldt 5159*, BO) near the western end of New Guinea (Fig. 1).

The peculiar morphology of the bud-bearing leaves of *Phanerosorus* has been given much attention in comparison with indeterminate leaves in Gleicheniaceae and *Lygodium* (Diels, 1902; Compton, 1909; Bower, 1926; Troll, 1939; Holtum, 1957). The leaf architecture of *Phanerosorus* was considered to be equivalent to that of *Lygodium* with pinnate bearing an at first dormant bud between a pair of pinnules. Such a comparison was based on study of mature plants of the better known *P. sarmentosus*, little information being available for *P. major*. The present study reveals that the leaf architecture in *P. major* is more complex than in *P. sarmentosus*. Also, heteroblastic series of leaves of *P. major* are described.

**Materials and Methods**

Ample material of *P. major* at various stages from juvenile to mature plants was collected in Seram (Ceram) Island, the Moluccas, East Indonesia (Fig. 1) during botanical field surveys in 1983 and 1985. This is the first report of the genus from that island. It grows locally abundantly on dry, almost vertical limestone cliffs at three not very

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remote sites in lower montane forest at elevations of 600–800 m in a ravine to the interior of Hatumete, Kecamatan (=County) Tehoru. Materials were fixed with FAA (formalin-acetic acid-alcohol solution) or dried for herbarium specimens. To observe venation the material was cleared with commercial bleach and stained with basic fuchsia. Voucher specimens were deposited in the Herbarium of the University of Tokyo (TI).

**Observations**

The rhizomes are to 2.5 mm thick, creeping and branching with clusters of living green and dry brown pendent leaves, and are densely covered with pale brown setae consisting of to 18 cells. Numerous juvenile plants grow on the same limestone cliffs and are associated with matted, slender ribbon-shaped gametophytes reproducing vegetatively. The gametophytes are also sometimes associated with the mature sporophytes. The gametophytes of *P. major* will be treated in a separate publication (YOROI and KATO, in prep.).

The leaves are to 65 cm long, including stipes to 15 cm long, and are to 30 cm broad. They are sympodially pinnate in general organization with to 7–8 laterals on each side of the main rachis. The leaf apex consists of 1–3 times forked pinnules (lamina-bearing segments). The laterals are alternate, to 3 cm apart, the few lowest usually deciduous. The pinnules of the laterals are simple or in large leaves usually once or twice forked, and petiolate or sessile. They are mostly 3–5 mm broad but sterile pinnules may be broader, to 6 mm. The pinnules have lamina about 0.3 mm thick and coriaceous, and the veins are hardly visible. The upper epidermis is polished with the outer cell wall about 5 μ thick. The lower epidermis (Fig. 4B) is dull brown and papillate with dense protruding, round papillae to 30 μ thick, and has stomata of anomocytic type (VAN COTTHEM, 1973).
The architecture of the laterals is variable. Fundamentally, each of them consists of a primary pinnule, which is sessile and has the outer laminar margin continuous with the rachis wing, as in *Lygodium* (Mueller, 1982), and either a bud at the axil or a secondary pinnule developed from the bud (Figs. 2A, 4A). The secondary pinnules are stalked and have the stalk wing not continuous with the rachis wing. Often the primary pinnules are lacking (Figs. 2B, 4A). The secondary pinnules bear a bud or higher order of secondary pinnule near the base of the stalk (Figs. 2B, 4A). All buds are densely covered with the same type of hairs as on the rhizome, but shorter and with fewer crosswalls.

In large leaves of mature plants, some laterals consist of buds alone, or simple or forked secondary pinnules at the axil of primary pinnules, or the others consist of secondary pinnules without primary pinnules (Figs. 2B, C). The secondary pinnule may bear a bud near the base of the stalk, or occasionally two buds or bud-derived pinnules on either side. The secondary pinnules usually have an organization similar to that of smaller leaves or primary pinnules, and sometimes are large enough to resemble mature leaves. The most complex laterals (Fig. 2C) consist of a secondary pinnule bearing several orders of secondary pinnules, each branching near its base. The highest order pinnule bears a bud near the base. The orientation of all the pinnules appears to be in the same plane.

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Fig. 2. Buds and secondary pinnules in *P. major* (Kato et al. C-1245). Buds are indicated by arrowheads. A. Bud at axil of primary pinnule (right). Note rachis-wing continuous with pinnule margin. B. Bud near base of secondary pinnule (left) on rachis. Note rachis-wing interrupted at insertion of pinnule (marked by arrow). C. Rachis and lateral (right) consisting of secondary pinnule with two higher orders of pinnules and bud near base of ultimate pinnule. Note rachis-wing interrupted (marked by arrow) at insertion of secondary pinnule.
Fig. 3. Ontogenetic series of leaves of juvenile plants of *P. major* (Kato et al. C-1245, C-7150). Arrowheads and asterisks indicate buds and secondary pinnules, respectively. Blades not marked by asterisks are simple juvenile leaves or primary pinnules.
as that of the parental leaves (Fig. 2C).

Leaves of juvenile plants (Fig. 3) are small and simple with a midrib or a pinnate vein system. As the leaves enlarge they may be forked, the larger leaves, whether simple or forked, bearing a bud on the rachis, usually at the upper part. This bud resembles buds not associated with primary pinnules in the mature plants. Occasionally a bud is borne near the base of the blade which is cut away at the insertion of the bud. A simple secondary pinnule may exist in the same position as a bud and differs from a primary pinnule by the presence of a stalk and interrupted wing as in mature plants. A bud may occur near the base of the stalk of a secondary pinnule. The larger leaves (Fig. 4A) are alternate pinnate with simple or forked terminal pinnules. A bud or secondary pinnule occurs at the axil of each lateral primary pinnule. Development of the secondary pinnules from the buds appears rather irregular, as compared with Lygodium.

Veins of juvenile leaves are simple or pinnate with simple lateral veinlets (Fig. 5A). Veins of the larger leaves consist of a midrib and once or twice forked lateral veinlets (Fig. 5B). The vein-endings join a false-vein running along the laminar margin, or may end short of the cartilaginous margin. The venation of soriferous pinnules is more complex. Veins are forked more times, and the sori are supplied by two or three lateral veinlets originating from adjacent branch veins (Fig. 5B).

The sori are round and covered by thick-stalked, peltate indusia. The indusia are dark-brown (when dried), thick, and hemispherical with fringed, pale brown, membranous margin. The margin is to 0.3 mm broad including fringes and narrower than that

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Fig. 4. Phanerosorus major (Kato et al. C-1245). A. Larger leaves of young plants. Arrowheads indicate primary pinnules and asterisk indicates secondary and higher order of pinnule. B. Lower epidermis with stomata. Arrows indicate transections of papillae.
of *P. sarmentosus* 0.5 mm broad or more. Up to 20 sporangia are attached in more or less regular two (upper and lower) layers on the receptacle of each sorus. The sporangia are short and thick-stalked with incomplete oblique annuli of 20–30 cells. Old, remaining receptacles are prominently raised (vs. slightly raised in *P. sarmentosus*). Spores are tetrahedral, trilete and transparent.

*P. sarmentosus.*—The leaves are pinnate with a pinnately lobed apex and alternate laterals each consisting of two opposite primary pinnules with a bud sunken in a crater between them. Each of the pair of primary pinnules is basally simple, bifid, or trifid, the segments simple to twice forked. The largest pinnules may be sympodially pinnate with a catadromic branching pattern (Fig. 6D). The rachis-wing is continuous with the laminar margin of both acrosopic and basiscopic primary pinnules. The bud may grow to become a secondary pinnule. Often a bud occurs near the base of the stalk of the secondary pinnule as in *P. major*. The upper laterals may consist of a solitary, simple or forked primary pinnule with a bud at the axil, as in *P. major*.

**Discussion**

*Phanerosorus major* was described from Waigeo Island by Diels (1932), who pointed out differences from the closely related *P. sarmentosus* in leaf morphology and anatomy. As far as the Seram specimens are concerned, although there is no diagnostic difference in the length, breadth, and thickness of the pinnule, it was confirmed that the densely papillate lower epidermis is a diagnostic character of *P. major*, as compared with hardly or not prominently papillate one in *P. sarmentosus*. Additional useful characters are sori, venation and the organization of the laterals of leaves. The membranous margin of indusia is narrower and the remaining old receptacles are more prominently raised than in *P. sarmentosus*. The sori are supplied regularly by two or three veinlets, as compared
Fig. 6. Diagrammatic illustrations of leaf ramification of Matoniaceae. A–C. Phanerosorus. A is usual structure of P. sarmentosus; B–C common in P. major. Asterisks indicate secondary pinnules and pinnules of higher orders, and broken lines in B, C presumed supressed primary pinnules. A. Leaf with laterals consisting of bud or secondary pinnule at apex between pair of primary pinnules. Bud may occur near base of secondary pinnule. B. Leaf with laterals consisting of bud or secondary pinnule at axil of primary pinnule. Buds of pinnules may occur near base of secondary pinnule. C. Leaf with bud on rachis (top) and leaf with laterals consisting of secondary pinnules bearing buds or pinnules of higher orders near base (bottom). D. Elaborate secondary pinnule of P. sarmentosus. E. Juvenile-leaf architecture of Matonia pectinata (based on Bower (1926) and Stokey and Atkinson (1952)). F. Matonia pectinata.
with *P. sarmentosus* in which sori are terminal on free veinlets or supplied by two, or rarely three (PRICE, pers. comm.) veinlets.

The leaves of *P. major* are more complex in structure than those of *P. sarmentosus*. The variations in leaf architecture are illustrated in Fig. 6A–C. The simplest architecture is expressed by the laterals consisting of a pair of primary pinnules and a bud or a bud-derived secondary pinnule at the apex (Fig. 6A), as in *Lygodium*. The secondary pinnules usually bear a bud near the base of the stalk. This is typical of *P. sarmentosus*. A presumed suppression of the acroscopic pinnule, typical of *P. major* and occasional in *P. sarmentosus*, results in a bud in the axil of the basiscopic pinnule (Fig. 6B). Suppression of the basiscopic pinnule leads to a lateral bud on the rachis (Fig. 6C), a condition exclusive to *P. major*.

*Lygodium* is radically different from *Phanerosorus* in anatomy, sori, sporangia, spores, and its scandent twining habit, so the remarkable similarity in branch pattern must surely be due to convergence. However, the branch pattern of *Phanerosorus* differs from *Lygodium* in that: (1) acroscopic, and often both acroscopic and basiscopic pinnules are lacking in *P. major*, and (2) buds are borne near the base of secondary pinnules and those of higher orders.

The leaf ramification of *Phanerosorus* was interpreted as a series of modified dichotomies and compared with that of *Matonia* (DIELS, 1902; COMPTON, 1909). However, *P. major* leaves develop from simple or forked directly to pinnate and undergo no dichotomous stage. They differ considerably from that of *Matonia*, in which juvenile leaves were observed to be once or twice forked with pinnate veins (Fig. 6E; BOWER, 1926; STOKEY and ATKINSON, 1952). They are considered to have been separate since the Triassic or Jurassic (ANDREWS and BOUREAU, 1970).

The sympodial leaf architecture of *Phanerosorus* as understood in this paper and the pedate, fundamentally pinnate organization of *Matonia* leaves with a terminal, pectinate pinna and a pair of lateral pinnae with several pinnules similar to the terminal pinna (Fig. 6F; TROLL, 1939; WAGNER, 1952) could be derived from a general pinnate structure, although some authors interpreted them as a series of unequal dichotomies (DIELS, 1902; COMPTON, 1909; HOLTUM, 1957). Therefore, a close relationship of Matoniaceae with Dipteridaceae with dichotomously organized leaves (e.g. COMPTON, 1909; COPELAND, 1947) is denied, in agreement with TROLL (1939) and WAGNER (1952).

We are thankful to Dr. M. G. PRICE of the University of Michigan for reading the manuscript with many invaluable suggestions, and Dr. K. UEDA and M. Sc. H. AKIYAMA of Kyoto University and Drs. U. W. MAHJAR of Herbarium Bogoriense for help in various ways. We are also indebted to the directors of the herbarium of Kyoto University (KYO) for the loan of specimens of Matoniaceae, and Herbarium Bogoriense (BO) for providing facilities. This study was supported by Grant-in-Aid for Overseas Scientific Field Research from the Ministry of Education, Science and Culture, nos. 58042006, 59041020 and 60043021.
November, 1985


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Shigeyuki Mitsuta: **Nine new records of ferns to Thailand flora** (光田重幸：タイ新産のシダ植物).

All collected in Phu Kradung during 1984 Oct. 30–Nov. 3, under co-operation of Kyoto University, Japan, and Royal Forest Department, Bangkok. Specimens cited in KYO.

**Dennstaedtiaceae**


*Murata et al. T-42452,* ca. 1200 m alt., in dense evergreen forest along stream.


*Murata et al. T-42445, T-42479, T-42547,* on rock in rather humid places in dense evergreen forest, ca. 1200 m alt.

This species is distributed from Himalayas to Taiwan through S. China and Indochina. This is the new record from Thailand, not only as to species, but also as to genus.

**Thelypteridaceae**


*Mitsuta et al. T-42394, T-42390,* on sandy bank of stream, ca. 1200 m alt.


*Murata et al. T-42031,* in hill evergreen forest, 900–1200 m alt.


*Murata et al. T-42426,* in dense evergreen forest, ca. 1200 m alt.

**Athyriaceae**


*Murata et al. T-42438, T-42747,* in dense evergreen forest along stream.


*Murata et al. T-42425,* in dense evergreen forest along stream, ca. 1200 m alt.

**Polypodiaceae**


*Murata et al. T-42834,* in dense evergreen forest along stream, ca. 1200 m alt.


*Murata et al. T-42162, T-42987,* on clayey wall at edge of hill evergreen forest, ca. 1200 m alt.

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