

Anatomical Studies of *Cyathocaulis naktongensis* OGURA from Central Honshu, Japan*

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(communicated by Kazuo ASAMA)

Introduction

The genus *Cyathocaulis* OGURA, a Mesozoic tree fern, has been known from several localities of Japan and the adjacent countries. Among four species of the genus, namely, *C. naktongensis* OGURA (1927 b), *C. tateiwai* (OGURA) OGURA (1938), *C. yabei* OGURA (1941 a) and *C. ogurae* HASHIMOTO (1971), *C. naktongensis* has the widest distribution, having been known from Arida, Wakayama Prefecture (OGURA, 1927 b) and Choshi, Chiba Prefecture (M. NISHIDA, 1962) in Japan as well as in Korea (OGURA, 1927 b, 1941 b). The specimen from Choshi, however, differs histologically from the type specimens of *C. naktongensis*, and represents a new species. Another stem of *Cyathocaulis*-type probably allied to *C. naktongensis* was reported from Tatsue, Tokushima Prefecture of Shikoku (OGURA, 1950). All Japanese specimens of *C. naktongensis* including the specimen from Tatsue occur in clastic rocks which had deposited in Early Cretaceous shallow marine basin. Similar clastic sequence of the same age is developed in the so-called Sanchu Graben in the Kwanto Mountains, so that the possible occurrence of *Cyathocaulis* from this area has been expected.

In November of 1976 the junior author found a piece of petrified stem of a tree fern (No. 80003) in a small valley near Sebayashi, Nakazatomura, Tanogun, Gunma Prefecture. After that he collected more than five specimens (No. 80004 and others), one of which was embedded in a greyish sandstone of the Lower Cretaceous Sebayashi Formation. In 1979 the senior author collected another stem (No. 80005) in another valley, Hachimanzawa. These localities are shown in Figure 1.

The Sebayashi Formation is divided into the lower and the upper members (MATSUKAWA, 1977). The lower member is dated as late Barremian to early Aptian, and yields many plant impressions (YOKOYAMA, 1894; OISHI, 1931; KIMURA and MATSUKAWA,

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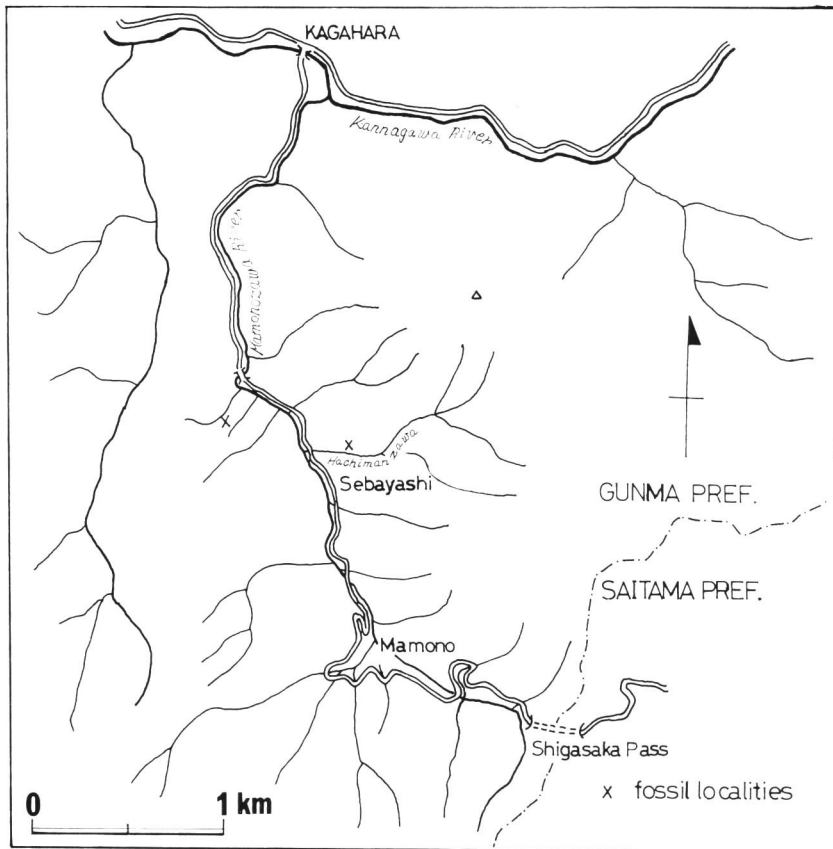


Fig. 1. A map showing fossil localities.

1979). The sediments which yielded our materials are located stratigraphically between the locality number 103 (late Barremian) and 209 (early Aptian) of the plant beds described by MATSUKAWA (1977) and KIMURA and MATSUKAWA (1979, fig. 2).

Some of the specimens were cut into pieces to obtain serial sections, and their micropreparations were made by either the thinning or the peel methods, for the latter 20 to 25 per cent HF solution was used as an etching reagent. They were anatomically compared with type specimens of all species of *Cyathocaulis*.

Our specimens of the stem show excellent internal structures, some of which are new to *C. naktongensis*, and we describe their histological details in this paper.

Results

Cyathocaulis naktongensis OGURA, J. Fac. Sci. Imp. Univ. Tokyo. Sect. III. 1 (3): 352. 1927, Bot. Mag. Tokyo. **55**: 454. 1941; Andrews in *Traité de Paléobotanique*. **IV**. fasc. 1: 316. 1970; OGURA, *Comp. Anat. Veg. Org. Pteridoph*: 366. 1972.

Specimens. Nine specimens were collected, of which three were numbered (No. 80003, 80004 and 80005) and examined. No. 80004 and a part of No. 80003 (both collected by Tanaka) are deposited in the National Science Museum under the registered number NSM-PP 7660 and NSM-PP 7661. No. 80005 and the micropreparations used in this study are deposited in the Laboratory of Phylogenetic Botany, Chiba University. Other specimens are deposited in the Chitose High School, Tokyo.

Locality. Sebayashi, Nakazatomura, Tanogun, Gunma Prefecture.

Horizon and age. Lower member of the Sebayashi Formation; late Early Cretaceous (Late Barremian to Early Aptian).

Distribution. JAPAN; Wakayama, Tokushima?, Gunma. KOREA; North Kyönsang Dô.

Description. External features: No. 80003. This is the largest specimen. Cross section is ovate, 24×15 cm in diameter including the root mass, and 12 cm in height.

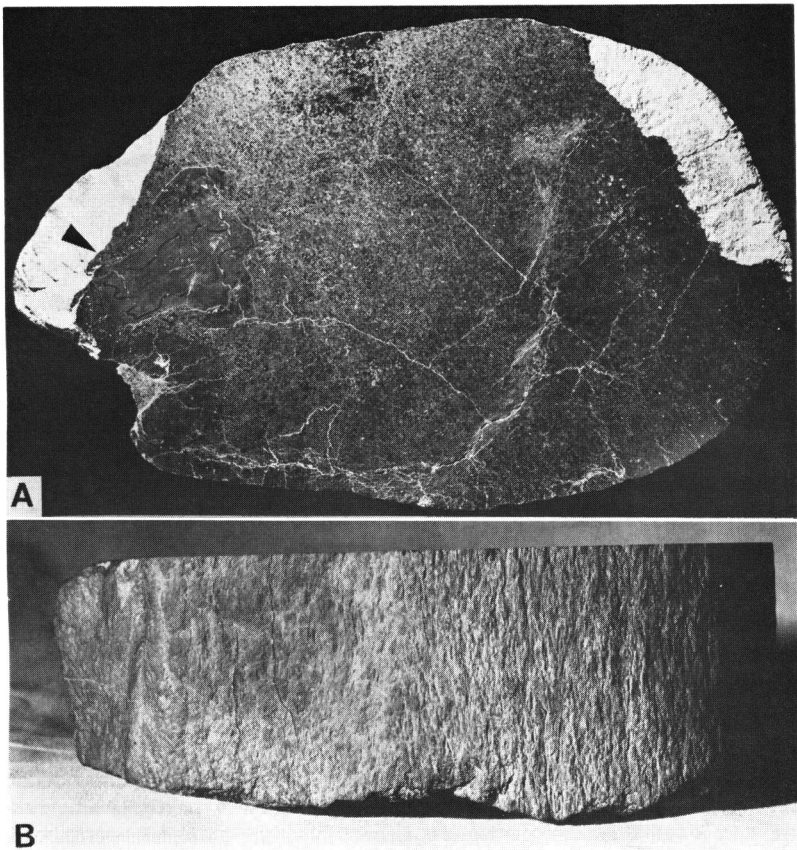


Fig. 2. *Cyathocaulis naktongensis* OGURA, No. 80003 (NSM-PP 7660). A, Cross section of the stem (arrow) and the surrounding root mass. B, Lateral view. All $\times 4/9$.

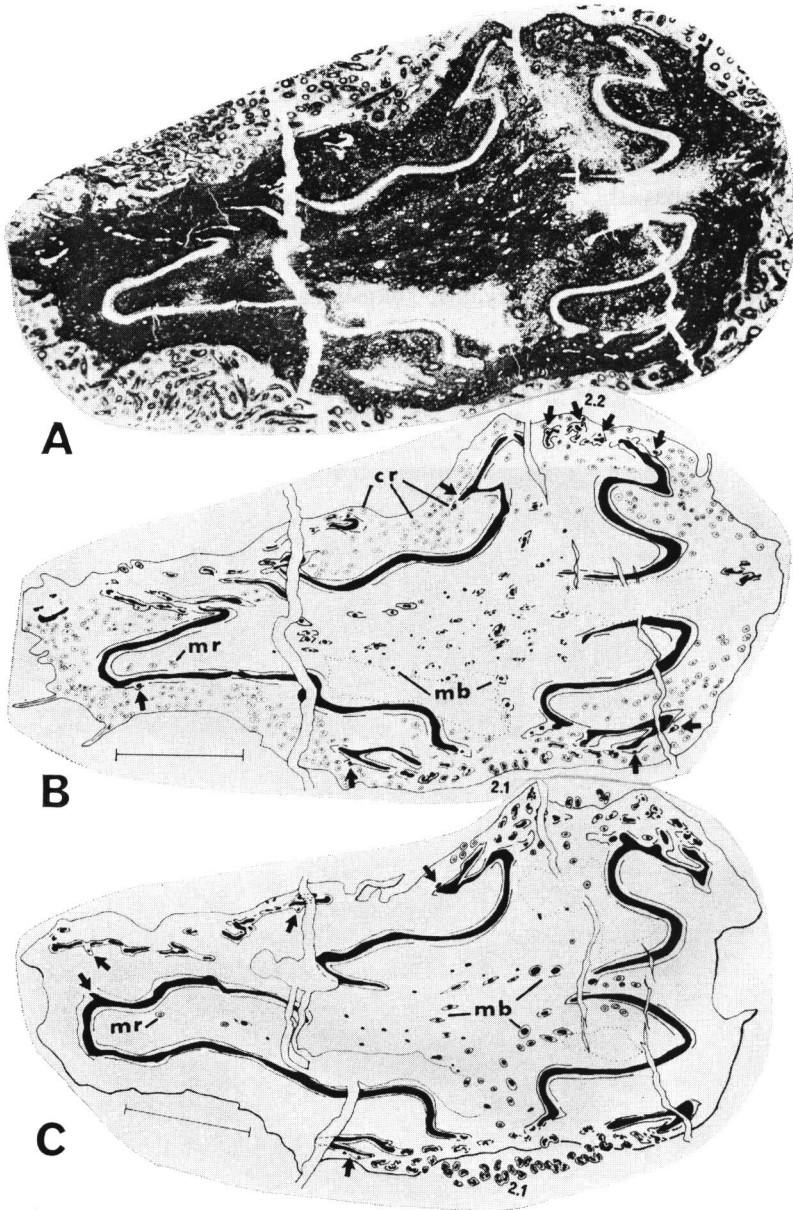


Fig. 3. *Cyathocaulis naktongensis* OGURA, No. 80003 (NSM-PP 7660). A, Cross section of the stem enlarged. B, Illustration of the same. C, Illustration of the stem a little distal level. Arrows in B and C indicate parting root traces. Numbers 2.1 and 2.2 correspond to the abaxial arc of the petiolar traces. cr: cortical root trace, mb: medullary bundle, mr: medullary root trace. All in the same magnification. Scales 1 cm.

The stele is 5.0×2.5 cm in diameter with seven leaf gaps and four meristelic bands (Figs. 2, 3).

No. 80004. This is the tallest one, 14.5 cm in height. Diameter is 4.5×7.5 cm at distal end, 8.7×7.5 cm at proximal end, both including the root mass. The stele is almost entirely preserved at the proximal end with the diameter 5.3×3.3 cm exhibiting 10 leaf gaps (probably 11 in a complete stele) and seven meristelic bands. At the distal end $3/4$ of the stele is lost by erosion. The specimen was cut into nine pieces to obtain serial cross sections (B-1 to B-9).

No. 80005. The stem is 7.0×10.5 cm in diameter including the root mass, 6.0 cm in height. The $1/5$ of the stele is lost, but is the largest of all, 6.5×3.5 cm in diameter with 10 leaf gaps and seven meristelic bands.

All of our specimens exhibit smooth surface of the stem, namely the leaf bases are flattened and never elevated as in *Cyathocaulis (Cibotiocaulis) tateiwai* (OGURA, 1941 b) and *C. ogurae* (HASHIMOTO, 1971).

On the dermal surface of the stem long multicellular hairs are perceptible (Fig. 4). They have been reported also in other species of *Cyathocaulis* except for *C. yabei* from Philippine in which the dermal layer was destroyed. Among the root mass surrounding the stem some hairy structures are often seen. A somewhat stout and short structure is the root hair (Fig. 4H), and a mass of long, much slender strings is the fungal hyphae (Fig. 4G). The former has been known also in *C. naktongensis* from Korea (OGURA, 1941 b).

Internal structures: The stem exhibits the same internal structures as of the type specimens of *C. naktongensis*. The meristelar margins curve inwardly to connect with the medullary bundles of which the larger are surrounded by the sclerenchymatous sheaths, while the smaller are not (Figs. 3, 4). Some of medullary bundles enter into the petiole to constitute the "median pairs" of the adaxial series of leaf traces as have been observed in *C. naktongensis* (OGURA, 1927 b) and in the living cyatheoid tree ferns (OGURA, 1927 a; LUCANSKY, 1974; LUCANSKY and WHITE, 1974).

Root traces are abundant in either the cortex or periphery of the pith. Serial cross sections of No. 80004 made us possible to know the origin and course of the root traces in the stem. The medullary root traces always originate from the inner side of the vascular bundle of the stem, while the cortical ones usually, but not always, from the outer side (Figs. 3, 4). The root traces, whether cortical or medullary, do not first exhibit actinostelic structure, a common root nature, but protostelic with a central mass of xylem surrounded by a phloem layer (Fig. 5A), when they are isolated from the meristele of the main axis. They soon become actinostelic with the diarch xylem.

Some of the cortical root traces originate directly from the leaf traces at the leaf gap. As the stele bulges out externally to form the abaxial arc of petiolar traces (inferior series), many root traces are separated from its outer periphery (Figs. 3, 4). The bulging-out of the stele then begins to divide itself into many isolated meristeles at its middle portion. These petiolar meristeles also separate more root traces which, however, along with the proximally parted traces, do not remain long in the cortex but

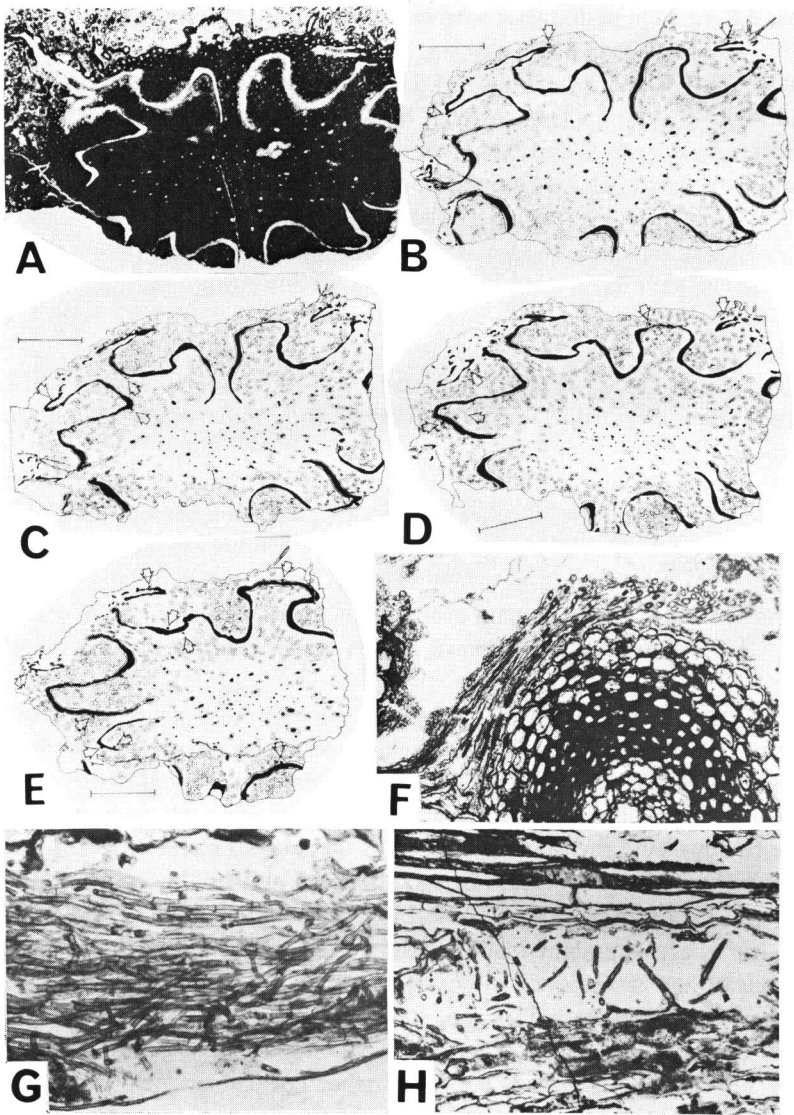


Fig. 4. A to E, Serial cross sections of the stem of *Cyathocaulis naktongensis* OGURA, No. 80004 (NSM-PP 7661). Distances in cm from the proximal end of the specimen are: 3.4, 4.8, 5.0, 6.3, and 8.2, respectively. Arrows in B to E indicate parting root traces. All in the same magnification. Scales 1 cm. F to H, Details of the external structures. No. 80003 (NSM-PP 7660). F, Dermal hairs. G, Fungal hyphae in the root mass. H, Root hairs shown in the longitudinal section of the adventitious roots. F, H $\times 53$; G $\times 213$.

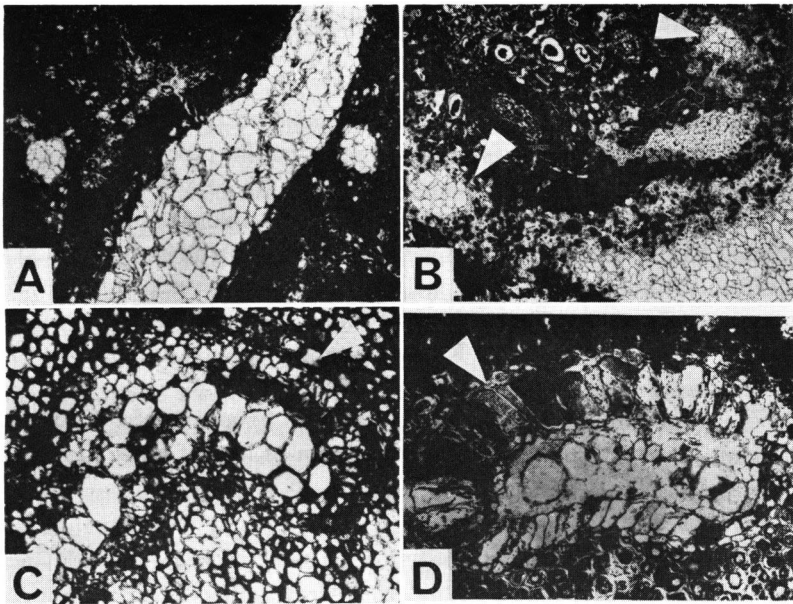


Fig. 5. Histological details of *Cyathocaulis naktongensis* OGURA, A, B. No. 80003 (NSM PP 7660), C, D. No. 80005. A, A cortical root trace (left) just after parted and a medullary root trace (right) parting from the same vascular bundle of the stem (center). Note protostelic nature of the root traces. B, Three cortical root traces (arrows) parting from the pointed tip of hook-shaped margin of the stelar bundle. See text for further explanations. C, Cross section of a leaf trace, showing small pericycle cells (arrow) and the mucilage cells filled with black contents, at the inner side of the pericycle. D, Another leaf trace showing large, radially elongated pericycle cells (arrow). A, B $\times 40$; C, D $\times 100$.

run outward to form a thick mass of adventitious roots around the stem.

When the abaxial arc of the petiolar strands is being separated from the stele of the stem, outer meristelar margins of the stem exhibit a pair of hook shape orientated face to face. Several small masses of vascular strands also depart from external pointed tips of the hook-shape (Figs. 3, 5B). OGURA (1941 a, b) described them as cortical bundles on the basis of their protostelic nature. However, it is certain from serial sections that these are not the cortical bundles but the cortical root traces, and their protostelic nature is a usual feature of the root traces just after detached from the stelar bundles (Fig. 5A). OGURA (1927 a, p. 180, fig. 15 A) illustrated an adventitious root of living *Cyathea spinulosa* near the place of parting which also shows protostelic structure. The cortical root traces also run outward to form the root mass.

The course of medullary root traces are somewhat complicated. Once they are detached from the stele, they never connect again with the stelar bundle. They run outward through the leaf gap in groups and enter the cortex passing a pair of openings between the abaxial and the adaxial groups of leaf traces. These openings correspond to the lateral infoldings of the petiolar bundle system. The root traces also enter the

cortex through parenchymatous tissue between the petiolar meristeles so as not to remain in the petiole.

The way of parting leaf traces does not differ much from that of the type specimens of *C. naktongensis*. The length of a leaf gap measured from serial cross sections of No. 80004 is about 13 cm which is very close to that of the type specimen of *C. naktongensis* (13 cm in specimen 2D from Korea). The length of a portion of a gap where its lateral margins curve inwardly to connect with the medullary bundles is about 4.5 cm.

A peculiar feature of our specimen is the presence of an adventitious bud as a long projection from the bulging-out of the stele which is later developed in the abaxial arc of petiolar traces (Fig. 4A). The presence of small stems in the root mass surrounding a large stem of *C. naktongensis* from Korea (specimen 2D, in OGURA, 1927 b) favors a general occurrence of the adventitious bud in this species.

Another feature of the petiolar traces is what can be seen in No. 80003, but with a little uncertainty owing to unfavorable preservation of its leaf base. In the leaf gap

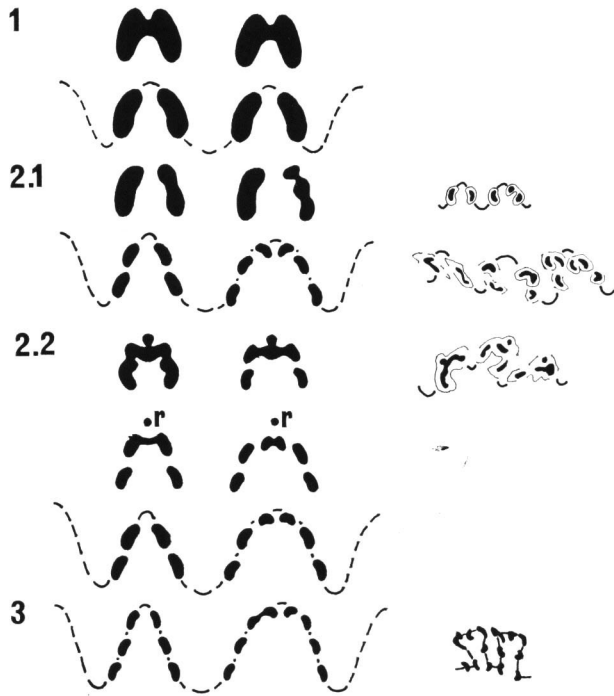


Fig. 6. Showing diagrammatically three types of wavy arrangements of the petiolar traces in the abaxial arc. 1, In living cyatheoids and perhaps in most species of *Cyathocaulis*. 2.1 and 2.2, In *Cyathocaulis naktongensis* OGURA, No. 80003 (NSM-PP 7660) described here. Numbers correspond to those in Fig. 3BC. 3, In *Yezopteris polycycloides* OGURA. Illustrations at right hand are examples actually observed in the specimens. See text for further explanations.

2.1 of fig. 3C the petiolar traces of the abaxial arc are arranged in a wavy but a little complicated row, which is referable highly complicated row of *Yezopteris polycycloides* OGURA from the Senonian of Hokkaido (NISHIDA, 1981 a; cf. Fig. 6), though the type specimens of *C. naktongensis* examined by us did not show so complicated manner as of our specimen. Some examples of leaf gaps such as 2.1 and 2.2 in Fig. 3BC may suggest the way the complicated wavy row was derived from the simple row represented by all living cyatheoid tree ferns and most species of *Cyathocaulis* (Fig. 6). *C. tateiwai* and *C. ogurae* exhibit the simple type of arrangement.

Histology. General histological features agree well with OGURA's description on *C. naktongensis*, for example, medullary bundles lacking the pith, parenchymatous ground tissue containing large secretory cells. Though petiolar bases are mostly decayed and lost, there are some petiolar traces being remained in the root mass (Fig. 5C). Some of them exhibit internal structures consisting of a central xylem plate, a phloem layer with large mucilage cells in the outer side of the metaphloem, a pericycle, an endodermis and a sclerenchymatous sheath, all surrounding the xylem concentrically in successive order. These features are in common with those of three species of *Cyathorachis* (NISHIDA, 1981 b) and of *Yezopteris polycycloides* (NISHIDA, 1981 a).

In our specimen the pericycle of the petiolar bundles show a remarkable feature. Some bundles possess small, thin-walled pericycle cells, while some possess radially elongated, thick-walled cells (Fig. 5CD). The radially elongated cells appear frequently in *Cyathorachis fujitana* OGURA em. H. NISHIDA, but not in other species of *Cyathorachis* (NISHIDA, 1981 b). They appear spontaneously in *Yezopteris polycycloides* (NISHIDA, 1981 a) as in our specimen.

Affinities. As is shown in Table 1, the histological and some morphological data such as the vascular formula (NISHIDA, 1981 b) suggest strongly that our specimen belongs to *C. naktongensis*. On the contrary complicated wavy arrangement of the abaxial arc of the petiolar strands could be a large morphological gap between our specimens and OGURA's, which is enough for one to separate ours as a different species. But, we put the present specimens in *C. naktongensis* until further evidences on the structure of petiolar bases will be accumulated.

C. naktongensis emended by M. NISHIDA (1962) included a specimen from Choshi. As its internal structures are totally different from the type specimens of *C. naktongensis*, it will be described later as a separate species.

C. tateiwai (OGURA) OGURA first described as *Cibotiocaulis* resembles histologically *C. naktongensis*, and M. NISHIDA (1962) included them in a sole species *C. naktongensis* emended. But, they are distinguishable from *C. naktongensis* by their external features. *C. tateiwai* has a rather slender stem, and its vascular formula at the leaf base is different from that of *C. naktongensis* which has a large number of traces (Table 1). The root mass of *C. tateiwai* is thin in contrast to the thick mass of *C. naktongensis*, so that the former stem is not a basal portion of the latter. We regard *C. tateiwai* as another species of *Cyathocaulis* from Korea.

Discussions. Relationship with *Yezopteris*: Though our specimens show a

Table 1. Comparisons of four species of *Cyathocaulis*.

Species (Locality)	Age	Pith in medullary bundle	Sclerenchymatous sheath of medullary bundle	Leaf base and the vascular formula (Nishida, 1981 b) at leaf base
<i>C. naktongensis</i> (Korea)	Early Cretaceous**	—	±	flattened 6(7)-14(15)-10-12(13)-40 and 7->10-10-13->36
<i>C. naktongensis</i> (Wakayama)	Early Cretaceous	—	±	flattened ?
<i>C. naktongensis</i> * (Chichibu)	Early Cretaceous	—	±	flattened ?-?-?->4->41
<i>C. tateiwai</i> (Korea)	Early Cretaceous**	—	+	raised 3-4-2-1(2)->8
<i>C. yabei</i> (Philippine)	Cretaceous?***	+	—	? ?
<i>C. oguræ</i> (Hokkaido)	Late Cretaceous	—	—	raised 4-9-6-3->14

* Present specimen.

** Originally described from the Upper Jurassic, but the plant bed is now regarded as the Early Cretaceous in age (CHANG, 1975).

*** OGURA (1941 b). While HASHIMOTO (1971) stated that the material was probably derived from Neogene beds.

slight similarity with *Yezopteris* in the arrangement of the “abaxial arc”, the general appearances of the petiolar strands of our specimens are still unknown. We can only suggest here a possible relationship of these Mesozoic tree ferns.

Relationship with living species: *Cyathocaulis* is similar to the living cyatheoids in its general arborescent habit, in the way of parting and the arrangement of leaf traces, and in having medullary bundles forming a network in the pith. But, the presence of hairs as dermal appendages which is a common feature of the dicksonioid tree ferns, the presence of medullary roots, and the deep incurvation of meristellar margins at the leaf gap are important morphological differences between *Cyathocaulis* and the living cyatheoids.

OGURA (1941 a) emphasized that *Cyathocaulis* possessed the cortical bundle and compared it with living cyatheoid stems having cortical bundles. However, it is evident that *Cyathocaulis* lacks the cortical bundle, and, moreover, the cortical bundle does or does not appear in the same genus of living cyatheoids. More fossil evidences will be requested in regarding *Cyathocaulis* as a direct ancestor of the living cyatheoids.

Other fossil stems: The tree fern stems with cyatheoid internal structures, that is, the dictyostelic stem with medullary bundles and with *Cyathea*-like leaf traces, are uncommon in the fossil records. *Dendropteridium cyatheoides* BANCROFT, *Alsophilocalis calveloi* MENENDEZ and *Cyathodendron texanum* ARNOLD are some of their representatives except for *Cyathocaulis* species. The stems of the former two Tertiary species from East Africa and Argentina respectively are anatomically similar to the living

cyatheoid stems, though neither hairs nor scales have been observed. *Cyathodendron* from the Eocene of Texas, United States, was considered to be allied to the Cyatheaceae by ARNOLD (1945). However, it has hairs instead of scales, and the way of parting leaf traces is so unique that it is difficult to find close relatives among fossil or recent species in the family Cyatheaceae.

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