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Root System of Tropical Trees 7. The Facultative Peg-Roots of *Anthocleista nobilis* G. DON

**Kořenový systém tropických dřevin 7.
Fakultativní kolíkovité kořeny u *Anthocleista nobilis* G. DON**

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Abstract — JENÍK J. (1971): Root system of tropical trees 7. The facultative peg-roots of *Anthocleista nobilis* G. DON. — Preslia, Praha, 43 : 97—104. — *Anthocleista nobilis* (*Loganiaceae*), a common tree in ombrophilous forests of Tropical Africa, develops both stilt roots and well-defined peg-roots in response to waterlogged soil and temporary flooding of the habitat. No root adaptations were found in specimens growing on normally drained ferrallitic soil. The peg-roots are facultative pneumorhizae remaining, within a certain habitat, constant in size and shape. Smooth and rough types of the peg-roots can be distinguished. Mature peg-roots are covered by suberized exodermis and/or by superficial periderm interrupted by numerous lenticels. The thick cortex contains large air spaces usual in similar kinds of pneumorhizae of tropical trees. The radial and terminal growth of the peg-roots is strictly limited. Two closely related species — *Anthocleista vogelii* PLANCH. and *A. liebrechtsiana* DE WILD. et TH. DUR — were found without any root adaptation to waterlogged ground.

Introduction

Among various root modifications studied by the research team of the Department of Botany, University of Ghana, the roots of *Anthocleista nobilis* G. DON provided most astonishing details about the plasticity and adaptive characters of roots in tropical trees. In a short paper presented to the Congress of the West African Science Association in Freetown, we have already published this interesting finding (JENÍK 1965). In the course of a post-congress expedition, we succeeded in observing the peg-roots of *A. nobilis* in the Central province of Sierra Leone, which confirmed our earlier assumption that these facultative organs develop in swampy forests all over Tropical West Africa. Later, during ecological work in various African countries, we have used all opportunities to study the growth habit of *Anthocleista nobilis* in diverse habitats. In addition, we could complete root observations on closely related *Anthocleista vogelii* PLANCH. and *A. liebrechtsiana* DE WILD. et TH. DUR. In the present paper, we attempt to summarize these observations.

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Distribution and growth habit of *Anthocleista nobilis*

Anthocleista nobilis G. DON (*Loganiaceae*) is a small tree of wide distribution in the forest zone of Tropical Africa. The area of distribution extends from Guinea in the west, to Nyassaland and Abyssinia in the east. The majority of authors describe the occurrence of *A. nobilis* in swampy sites along forest streams, and in secondary forests. In Ghana, THOMPSON (1910 : 178) has noted *A. nobilis* as species composing "edaphic formation" of the fresh-water swamp forest. TAYLOR (1960 : 44 et 52) regards this species as a small tree of secondary scrub. In Gabon, CHEVALIER (1916 : 277) listed *A. nobilis* as "common in all forests". Within the whole of West Africa, SCHNELL (1950 : 244) describes *A. nobilis* as species of moist sites, mainly in secondary formations.

According to our experince, in virgin forests *Anthocleista nobilis* primarily occurs scattered in swampy habitats along streams in the high forest zone. Occasionally, small trees of this species appear in groups in natural clearings. In vast areas of secondary forests disturbed by farming, mining and felling, *A. nobilis* is fairly common. With its large leaves (up to 2 m length) arranged on twigs in characteristic terminal clusters, this tree is readily distinguished in the tangle of the tropical forests. Next to *Musanga cecropioides* R. BR., this species is a familiar feature well known to travellers along major roads and tracks in the forest zone. The English name "Cabbage Palm" suggests its popularity, too.

Well-drained ferrallitic soils (ochrosols, oxysols) as well as various kinds of gleisols are represented in forests where *Anthocleista nobilis* occurs. *A. nobilis* could by no means be regarded as strictly hygrophilous species. Its wide amplitude of habitats was a puzzle in our root observations. Another trouble arose from the difficulty in the identification of *Anthocleista* species. In West Africa, *Anthocleista vogelii* and *A. liebrechtsiana* are closely related species with similar growth habit and similar environmental requirements. Careful checking of the specimen trees was necessary during the fieldwork.

Materials and methods

Following the first finding of the peg-roots of *Anthocleista nobilis* in the vicinity of Kade, Ghana, we observed the same organs on wet sites in many parts of the Tropical West Africa. At the same time, we failed to find the peg-roots on normally drained soils. In the following list, only those sites are quoted which provided morphological and anatomical materials described in the paper.

S-1: Swampy forest near the Kadewa Stream, western margin of the Agricultural Research Station in Kade, Southern Ghana. The soil is composed of grey mottled brown silty clays, moderately acid in the topsoil ("acid gleisol" sensu BRAMMER 1962). The swamps are densely covered by forest with predominating *Raphia hookeri* MANN et WENDL., *Carapa procera* DC., *Berlinia auriculata* BENTH., *Alstonia boonei* DE WILD., *Mitragyna stipulosa* (DC.) O. KTZE., *Ancistrophyllum opacum* (MANN et WENDL.) DRUDE. Older *Anthocleista* trees up to 20 m high and 0.4 m in diameter. Scattered on the ground, partly covered by decaying litter, partly hidden in clusters of peg-roots of *Raphia hookeri*, partly protruding from little pools of the flood-plain (see Pl. X. : 2). Both the "smooth" and "rough" type of the peg-roots is represented. (Locus classicus of the facultative peg-roots in *Anthocleista nobilis*.)

S-2: Forest clearing in the forest of the same area quoted above. The soil is normally drained ferrallitic soil ("forest ochrosol" sensu BRAMMER 1962), characterictic for the mesophilous rain forest. Secondary forest composed of *Alchornea cordifolia* (SCHUM. et THONN.) MUELL. ARG., *Musanga cecropioides* R. BR., and young trees of *Anthocleista nobilis* (10 m high, 10 to 20 cm in diameter). No peg-roots were found in *A. nobilis*. Only in one tree growing on the margin of a track, were short peg-roots developed on the swampy bottom of a ditch.

S-3: Secondary scrub on the flood-plain of the Teye River, near the bridge on the road from Magburaka to Bo, Central province of Sierra Leone. Waterlogged soil with ground water near the soil surface. Patchy tree layer composed of *Mitragyna stipulosa* (DC.) O. KTZE., *Musanga cecropioides* R. BR., *Elaeis guineensis* JACQ., *Raphia hookeri* MANN et WENDL.;in the shrub and herbaceous layer *Mussaenda afzelii* G. DON, *Lygodium cernuum* LINN., *Anchomanes difformis* ENGL., *Selaginella myosurus* (SW.) ALSTON, etc. Numerous *Mitragyna* specimens form abundant knee-roots, a well defined kind of pneumorhizae described by RICHARDS (1952 : 75). Young *Anthocleista nobilis* trees develop larger peg-roots ("smooth type") dispersed in the tangle of forbs and grasses.

S-4: Secondary forest not far from the road in the Tano-Nimiri Forest Reserve, Western Ghana. On the bottom of a valley, young *Anthocleista nobilis* trees possess stilt roots associated with numerous peg-roots ("smooth type") which can be observed only after careful removal of forbs, mainly *Cyclosorus striatus* (SCHUM.) CHING. and *Cyrtosperma senegalense* ENGL. See Pl. IX. and Pl. X : 3.

S-5: Swamp forest near Tarkwa, on the road between Tarkwa and Asankrangwa, Western Ghana. Forest heavily disturbed by felling. After careful examination of the ground, little peg-roots scattered among herbs and undecomposed litter could be observed and identified as organs of *Anthocleista nobilis*. Peg-roots of *Raphia hookeri* also present.

S-6: Fringing forest in the Ankasa Forest Reserve, Western Ghana. Peg-roots of *Anthocleista nobilis* developed only in the vicinity of streams and pools. The size and shape of the peg-roots apparently influenced by soil conditions. Both "smooth" and "rough" type of peg-roots observed. Trees on elevated ground outside the influence of flooding remain without peg-roots.

S-7: Secondary swampy forest near the road Cotonou to Abomey, 15 km south of Abomey, Dahomey. Scattered young trees of *Anthocleista vogelii* PLANCH. examined as to their growth habit and root system. Neither stilt-roots nor peg-roots observed.

S-9: Swampy site on the top of the Atewa Range, Ghana, approx. 840 m alt., with an isolated *Anthocleista nobilis* tree amidst a dense growth of *Marantochloa purpurea* (RINDL.) MILNE-REDH., *M. mannii* (BENTH.) MILNE-REDH., *Ataenidia conferta* (BENTH.) MILNE-REDH., *Staurogyne paludosa* (MANGENOT et AKÉ ASSI) HEINE, etc. Scattered peg-roots of *A. nobilis* in a moist depression protruded 5 cm above the ground.

As in our earlier work dealing with the tropical roots, emphasis has been placed on the external morphology, anatomy and analysis of the growth stages of the roots of *Anthocleista nobilis*. Numerous partial excavations of root systems were needed in order to ascertain the doubtless identity of the peg-roots. Free-hand sections were used to study the anatomical structure. As emphasized by GILL and TOMLINSON (1969 : 1), even elementary aspects of the growth habit of tropical trees remain unobserved and require further investigation.

Morphology of roots

In a species with wide ecological amplitude any description of "normal" features of the root system is next to impossible. A general picture of the roots cannot avoid references to particular environmental conditions.

Our excavations **(S-1, S-2)** show that the subterranean roots of *Anthocleista nobilis* spread in the surface layers of the gleisols and ochrosols, and produce few sinkers in the subsoil. Most of the horizontal roots are found within the upper 20 cm layer. In the wet ground, the position of these subterranean roots is controlled both by the texture of the soil, and by the fluctuating water. Loose sandy soils affect deeper position of roots; compact clays keep the horizontal roots close to the surface.

The distal rootlets (end roots) are distinguished into macrorhizae and microrhizae, a feature more or less defined in most of the dicotyledonous trees. With their large apices, the macrorhizae show more vigorous growth and actively extend the rhizosphere of the tree. The microrhizae are smaller laterals with limited radial growth, serving as feeding organs. Well defined macrorhizae develop adventitiously on the lower part of the bole, giving rise to stilt roots. When distally anchored, these roots maintain their characteristic of a macrorhiza even under the ground; all their laterals tending to form peg roots can be classed as macrorhizae, too **(S-4)**.

Though relatively rare, the stilt roots in *Anthocleista nobilis* are a recognized feature. For example, SCHNELL (1950 : 145), KUNKEL (1965 : 38 et 242 : Pl. 5), and VOORHOEVE (1965 : 50) listed *A. nobilis* among trees developing adventitious stilt roots at the base of the trunk. Only older trees with larger trunks are supposed to form these roots. In our material, even smaller trees with stems under 5 cm in diameter formed stilts **(S-4)**; see Pl. IX. These stilt roots anchor in soil and grow down into a depth of about 10 to 20 cm where they gradually turn into horizontal direction. Taking into account the exceptionally heavy crown with the huge terminal cluster of leaves, we can take these stilt roots as a successful adaptation ensuring the stability of the tree.

In waterlogged soils, bigger horizontal roots develop negatively geotropic laterals penetrating towards the soil surface and protruding several centimetres above the ground surface **(S-1, S-2, S-3, S-4, S-6)**. Externally, their structure, branching and coloration resemble that of the peg-roots of *Avicennia* spp. growing in the mangrove woodlands. However, contrary to these *Avicennia* trees, as well as *Voacanga thouarsii* Roem. et Schult., and *Raphia* palms in African swamps, the peg-roots of *Anthocleista nobilis* are inconspicuous and hardly visible in the undergrowth of the mixed stands of swamp forest. The brownish green or green peg-roots of this species are scattered in the litter and among herbaceous plants, and unless intentionally searched, they escape one's attention. This is, probably, the main reason why this peculiar root adaptation of a familiar African tree remained unknown to botanists and foresters.

Though variable in size and form, the peg-roots of *A. nobilis* keep certain characters by which these organs can be distinguished from other pneumorhizae in African swamps. Within a given habitat, the diameter and height of the peg-roots remain similar in size. Obviously, their radial and longitudinal growth is strictly limited. In average, these organs are 0.3 to 0.6 mm thick. The constancy of the thickness seems to be supported by the superficial formation of the periderm (see below), and by the thick cortex which can "absorb" the extension of the secondary tissues produced by the vascular cambium.

The height reached by the peg-roots ranges between 3 to 20 cm limits. However, the total length of the peg-roots is larger because of the subterranean portion. Again, the subterranean portion is affected by the depth of the horizontal mother root which varies between 5 and 20 cm. The total length of the pneumorhizae seldom reaches 30 cm.

The total length of the peg-roots and the proportion of their subterranean and aerial parts are affected by the environment and age of the tree. Old trees in the compact mud develop shorter peg-roots of smaller diameters **(S-1, S-5, S-6)**. The fluctuating water and floods affect the size of the pneumorhizae in the same direction. During the rainy season we have regularly found protruding peg-roots just one or two cm above the water level of the pools **(S-1)**. A sort of floating of these organs could be anticipated, and after the flood, the elongated peg-roots were changing into procumbent organs.

In younger trees growing in loose sandy soils, the peg-roots were found to be stout and to possess smooth surface, straight shape, and upright position **(S-3, S-4)**.

Though a gradient of transition forms could be found, two types of the peg-roots were distinguished: the "smooth" type with straight and smooth appearance, and the "rough" type with rugged surface and curved axis. The "rough" type appears to be the result of adverse environmental conditions, namely, more frequent flooding and browsing animals.

Under normal conditions the aerial portion of the peg-roots of *Anthocleista nobilis* remains unbranched. Occasional branching occurs after mechanical or physiological injury of the apex. In our material **(S-2, S-6)**, branching seemed to be the product of browsing animals. The restitution of an injured peg-root has the characteristic of direct or indirect regeneration.

On the subterranean portion, however, laterals of smaller diameter occasionally develop (see Pl. XI.). They can be branched several times, and their distal portion possesses the form of microrhizae, i.e. a characteristic form of the feeding roots.

Numerous lenticels which disrupt the periderm on the aerial portion of the peg-root are a very characteristic feature. Their number and size vary according to soil and water conditions. We could observe that in very wet sites and temporary pools within the swamps, the white tissue of the lenticels grew vigorously and was bulging out of the root-surface **(S-1, S-6)**. Pl. X : 2 gives a picture of the lenticels on the peg-roots protruding above the water level of a pool. The profuse development of lenticels provides a certain character in the recognition of the *Anthocleista nobilis* peg-roots, e.g. against the peg-roots of the palms (*Raphia* spp., *Ancistrophyllum* spp.) growing in their association. Remarkably, ADAMSON (1955 : 155) described peg-roots in dicotyledonous *Terminalia arjuna* BEDD in the Far East without lenticels at all.

The area of distribution of peg-roots around a tree, obviously, depends on the age and size of the tree. In isolated specimens growing amidst mixed forest, peg-roots could be observed as far as 20 m apart from the trunk **(S-1)**. In young trees, the peg-roots are limited to the closer neighbourhood of the stem and grow in apparent dependence on the stilt roots **(S-4)**.

Anatomy of the peg-roots

The morphological variability of the peg-roots of *Anthocleista nobilis* correspond with the variability of their anatomical structure. A satisfactory assessment of this variability, however, would require a special study in the future. In spite of larger excavations, early stages of the development of the peg-roots, i.e. newly formed pneumorhizae with young apices, were missing in our material collected in West Africa. Thus, the following account describes merely the structure of the mature stage of "smooth" peg-roots **(S-4)**.

The peg-roots develop in sequence from endogenous primordia in the pericycle of the horizontal roots. After full disintegration of the epidermis, the subterranean portion of the peg-root is covered by a layer of exodermis, under which two or three layers of ill-defined periderm occur. The thick cortex occupies nearly 2/3 of the radius, and its structure is dominated by loose parenchymatous tissue with large air spaces arranged in radial direction. The vascular bundle contains 16 to 20 poles of primary xylem. The vascular cambium, though distinguishable, is at the beginning of its function, the secondary tissues being still very small. The pith contains large cells with dark contents, and its cell-walls get partly lignified.

The aerial portion of the peg-roots is also covered by 1 or 2 layers of an exodermis. The periderm is well-defined: the phellem consists of 3 to 5 layers, and even a phelloderm can be differentiated. Large lenticels of about 1 mm length and 0.5 mm width disrupt the periderm. The thick cortex contains air spaces on a smaller scale than that observed in the subterranean portion. The endodermis is still visible. The primary vascular bundle contains 16 to 20 poles. The vascular cambium appears to be in a more advanced stage of activity, and correspondingly, the secondary tissues are better developed. Their size is affected by the distance from the apex. Large pith contains cells with highly lignified cell-walls.

The superficial periderm stretches up to the apical zone which is also covered by a cork layer. In most cases, the activity of the apical meristems seems to be terminated. In a few cases, renewed terminal growth could be observed, which was marked by the disrupted cork sheath below the apex.

As was mentioned in the preceding description, the development of the superficial periderm beneath the exodermis is a characteristic anatomical feature of the peg-roots of *Anthocleista nobilis*. Similar development in secondary growth of the root is common in aerial roots of many African trees. The superficial exodermis was described in a great detail in *Avicennia germinans* by CHAPMAN (1944 : 511—523). In the pneumorhizae of *Terminalia arjuna*, however, the periderm develops in the pericycle (ADAMSON 1955 : 151), as is usual in the majority of underground roots of the trees.

The superficial formation of the periderm, the cork sheath on the apex, the sluggish activity of the vascular cambium and stillstand of the apical meristems result in the limited size of the entire organ, and the pencil-like characteristic is maintained throughout the life span of the pneumorhiza. This is a substantial difference as against the peg-roots of *Sonneratia* spp. in the eastern mangrove woodlands.

Roots of other *Anthocleista* species

In the course of our root studies in *Anthocleista nobilis*, two closely related species — *A. vogelii* and *A. liebrechtsiana* — were also examined. Among tropical trees, many types of pneumorhizae are represented in all related species within the respective genus, e.g. peg-roots in *Avicennia* spp., spine-roots in *Macaranga* spp., stilt roots in *Uapaca* spp., etc.

Our effort was supported by the fact that *Anthocleista vogelii* and *A. liebrechtsiana* are described by many authors as trees closely associated with swampy sites (SCHNELL 1950 : 244; IRVINE 1961 : 600—601). As indicated above, the identification of various *Anthocleista* species according to vegetative characters proved to be a fairly difficult problem. We could distinguish the relevant species only after long experience with flowering specimens.

Isolated populations of *Anthocleista vogelii* could be studied at a locality in Dahomey **(S-7)**; pure population of *A. liebrechtsiana* was examined in Southern Ghana **(S-8)**. On both sites, conditions were very favourable to the development of pneumorhizae, however, no kind of root adaptations could be observed. This experience seems to be confirmed by JACKSON (1964 : 98) who failed to find any marked adaptative features in *Anthocleista vogelii* in Nigeria.

Without proper justification HALLÉ et OLDEMAN (1970 : 36—37) have transferred our findings of pneumorhizae in *Anthocleista nobilis* to *A. procera* LEPRIEUR. The latter species, however, has not been collected in Ghana, hitherto, and we had no opportunity to examine this species in the field. *A. procera* is a tree without spines (LEEUWENBERG 1961 : 31) and in contrast to this, our specimen trees observed in Ghana and Sierra Leone showed two spines above the leave axils and on the trunks.

Ecology of the peg-roots

The formation of peg-roots in *Anthocleista nobilis* is an ecological phenomenon, par excellence. The wide range of environmental conditions in which this species occurs gives a good opportunity for the assessment of decisive factors influencing the development of pneumorhizae in tropical forests. In mangrove woodlands, for example, the soil composition may vary considerably, yet, their periodical flooding by tidal waters, and the salinity of the sea water make the habitats of this vegetation fairly uniform. Thus, the impact of the environment on formation of the pneumorhizae remains obscure. A similar difficulty arises with the explanation of the growth habit in trees of fresh-water swamps. The majority of trees listed as species with one or other kind of pneumorhizae are hygrophilous species limited to wet soils (see a list in OGURA 1940).

For example, *Mitragyna* spp. and *Raphia* palms, all strictly hygrophilous species in the fresh-water swamps of Tropical Africa, develop familiar pneumorhizae, the formation of which cannot be easily interpreted in ecological terms. Nevertheless, we can assume that the breathing roots may not develop in parts of their root system stretching over the dry ground, and in some specimens, possibly, may not develop at all. This is, however, difficult to ascertain and many authors, actually, regard the pneumorphizae of the mangroves and hygrophilous trees of fresh-water swamps as more or less obligatory vegetative organs.

Observations in *Anthocleista nobilis* prove that peg-roots are not, necessarily, an obligatory component of the growth habit of this species, and that these organs may not develop under certain environmental conditions. On normally drained soils the peg-roots are always absent **(S-2, S-6)**; on gleisols with fluctuating water level, the peg-roots were always present **(S-1, S-3, S-4, S-5, S-6)**. An interesting case was observed in the forests near Kade **(S-2)**: in the area of well-drained ferrallitic soil, several peg-roots appeared on the bottom of a ditch along the track.

The contingency in the formation of the peg-roots in the aforementioned species make it easier to interpret these adaptive organs in proper ecological way. The cardinal point in any adaptation is the question: adaptation to what? The obvious contrast between sites with peg-roots and sites without peg-roots suggests that these organs are, primarily, an adaptation to soils lacking sufficient aeration. In gleisols the available nutrients are more abundant than in elevated parts of the soil catenas; the aeration appears to be the factor in minimum affecting the plant growth. The ultimate position of the mature peg-roots protruding into the open air, as well as their anatomical structure with large cortical air spaces and numerous lenticels also suggest that the critical factor in question is, possibly, aeration necessary for free exchange of oxygen and carbon dioxide between the living roots and surrounding environment.

The notion that the pneumorhizae of *Anthocleista nobilis* may serve as organs actively spreading the feeding roots into the fertile upper layers of the soil is hardly acceptable in our case (compare the discussion of the function of the pneumorhizae in Chapman 1944). The rate of soil acretion in the flood-plains of small streams in the rain forest is very limited; the rate of the decomposition of the litter, on the other hand, is fairly high. Moreover, why should a substantial portion of an organ assumed to spread the feeding roots in topsoil protrude into the open air above the ground?

Finally, the morphological variability of the peg-roots in *Anthocleista nobilis* is of ecological interest. The size and shape of these organs are in good correlation with soil features. Compact mud composed of clay particles affects the development of thinner and rougher pneumorhizae; light sandy soil and loose organic detritus produce smooth peg-roots of larger diameter. This is in full agreement with usual phenomena observed in the ecology of subterranean roots in Central European trees: in compact soils smaller apices and end-roots can better overcome the resistance of the tough soil environment. The smaller apices, naturally, give rise to smaller stele and smaller cortex.

In conclucion we should like to emphasize the meaning of the attribute "facultative" in connection with the peg-roots of *Anthocleista nobilis:* Though the contingency of formation of various pneumorhizae in many tropical trees could be anticipated, *A. nobilis* actually appeared to be the first species in which the facultative nature of the breathing roots was beyond any doubts.

Souhrn

V článku jsou popsány kolíkovité dýchací kořeny (kolíkovité pneumorhizy) u stromu *Anthocleista nobilis* G. DON z čeledi *Loganiaceae*. Jmenovaný druh roste v lesích rovníkové Afriky a má širokou ekologickou amplitudu, zahrnující propustné ferralitické půdy i nepropustné glejové půdy. *A. nobilis* je zároveň i velmi známou dřevinou, běžně rozeznávanou podle habitu ve smíšených tropických lesích. Kolíkovité dýchací kořeny vznikají u tohoto stromu výhradně na dlouhodobě zamokřených stanovištích s nepropustnou anebo zaplavovanou půdou. Podle morfologické i anatomické stavby jsou tyto kořeny vyhraněnými orgány, přirovnatelnými po mnoha stránkách ke známým pneumorhizám rodu *Avicennia* v mangrovových lesích. Kolíkovité kořeny vznikají endogenně v pericyklu horizontálních kořenů. Rostou negativně geotropicky směrem k povrchu půdy a posléze vyčnívají několik centrimetrů až decimetrů nad povrch půdy. Jsou morfologicky proměnlivé (hladké a drsné typy), avšak jejich variabilita nepřekračuje hranice tvarově vyhraněného orgánu, jehož tloušťkový i délkový přírůst je omezený. Kolíkovité kořeny u *Anthocleista nobilis* bývají celkem až 30 cm dlouhé (podzemní + vzdušná část) a 0,3 až 0,8 cm tlusté. Tvoří periderm v povrchových vrstvách primární kůry. Nadzemní část mívá zvlášť četné čočinky. V primární kůře starších a podzemních úseků jsou vytvořeny velké vzdušné prostory. Hladký typ kolíkovitých kořenů se tvoří zejména u mladších stromů na lehkých písčitých půdách nebo v kypré hrabance krátkodoběji zamokřených stanovišť. Drsný typ se tvoří na slehlých jílovitých a dlouhodobě zamokřených půdách. Podle přítomnosti či nepřítomnosti kolíkovitých kořenů na různých stanovištích můžeme tyto orgány druhu *Anthocleista nobilis* s velkou pravděpodobností považovat za adaptaci na špatně provzdušněné zamokřené půdy. Jsou to výrazně fakultativní orgány, které zcela chybí u stromů rostoucích na normálně propustných půdách. U příbuzných druhů *Anthocleista vogelii* a *A. liebrechtsiana* nebyly kolíkovité dýchací kořeny nalezeny.

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Recensent: Z. Černohorský

See also plates IX.—XI. in the appendix.

Photo 1. — General view of the growth habit of a young *Anthocleista nobilis* in a swamp in the Tano-Nimiri Forest Reserve, Ghana. The length of the scale at the foot of the tree equals 1 m. A detail of the peg-roots developed in the same tree is given on the Pl. X. : 3.

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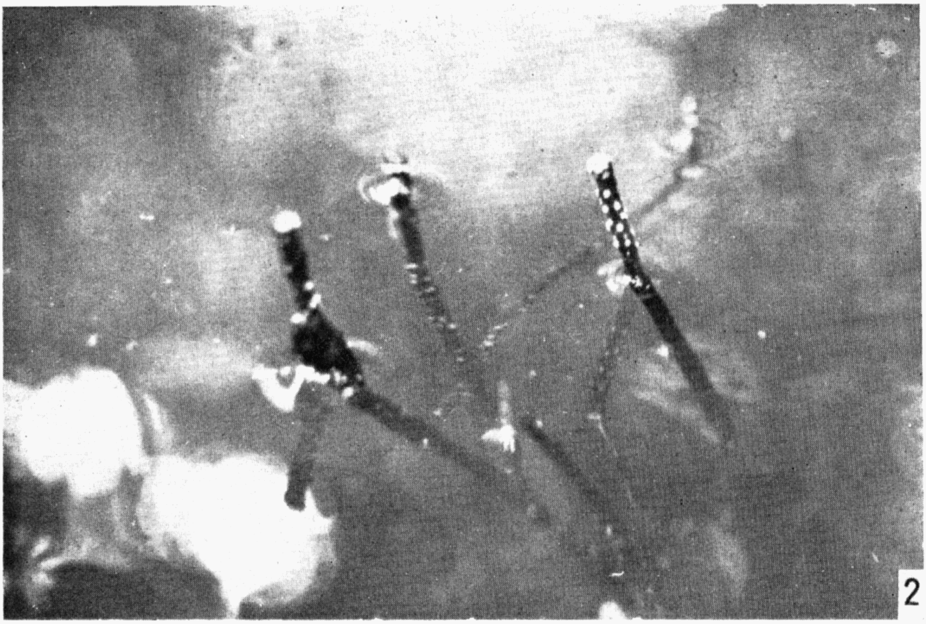

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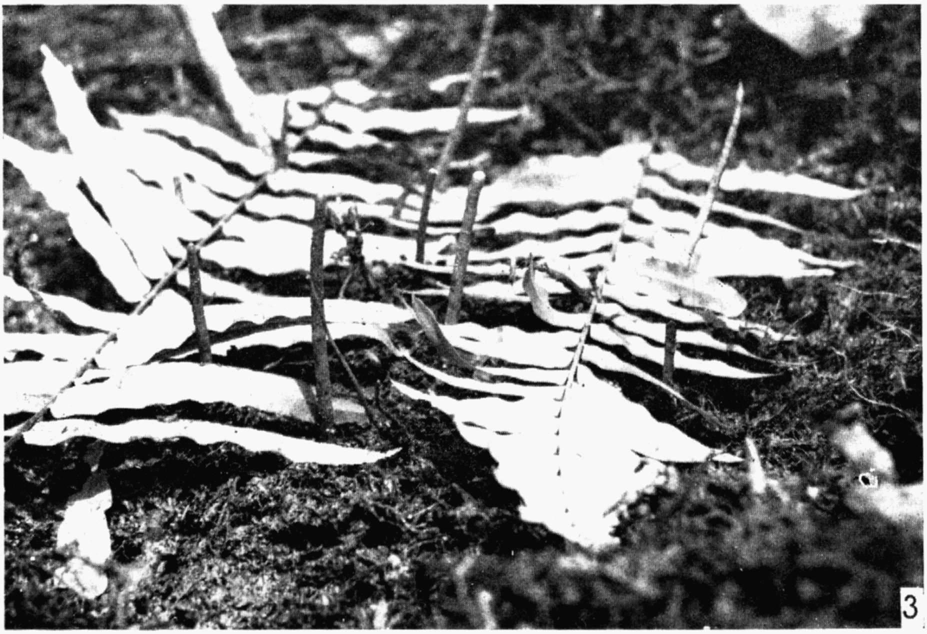

3

Photo 2. — The peg-roots of *Anthocleista nobilis*, protruding above the water level of a temporary forest pool after a period of rains ("rough" type of the peg-root).
Photo 3. — A detail of the "smooth" type of peg-roots developed at the foot of a young *Anthocleista nobilis* in the Tano-Nimiri Forest Reserve (see the general habit of the tree on the Pl. IX. : 1). The fronds of the fern *Cyclosorus striatus* spread over the ground to make the peg-roots visible.

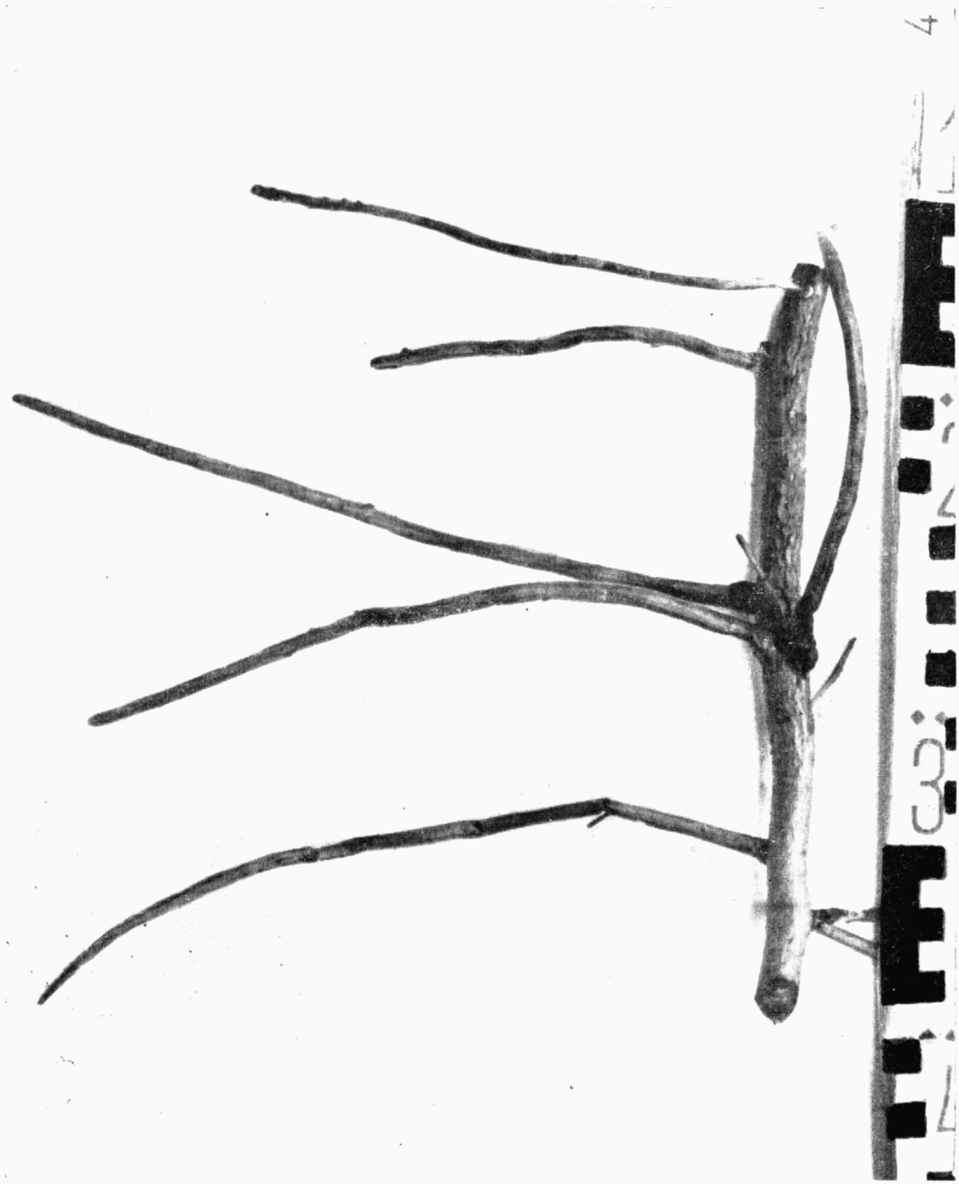

Photo 4. — General morphology of the peg-roots of *Anthocleista nobilis*, excavated from the soil. Note the constant diameter and similar length of the whole set of pneumorhizae attached to a portion of thicker horizontal root. The intervals of the scale are in centimetres.

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