Morphology and Development of the Sinker in *Pecteilis radiata* (Orchidac.)

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Ogura (1953) studied the comparative morphology and anatomy of the sinkers of 27 species belonging to 10 genera of the Ophrydinae, and discussed the morphological nature of the organ. In his paper, the vascular behaviours within the full-grown sinker were examined. However, the sinker development, most significant in understanding the morphological nature of the organ, was not studied in any species.

The sinker development of the Ophrydinae was studied first by Irmisch (1850) in *Platanthera bifolia*, later by Nothdurft (1955) in a species of *Serapias*. Between the two, there were some descriptions, among which Sharman's (1939) on *Orchis mascula* entered in details. In the present paper the sinker of *Pecteilis* (*Habenaria*) *radiata* Rafin. is described which somewhat differs from that of *Orchis mascula* in respects of morphology and development.

**Material and methods**

The plant grows wild in the vicinity of Nagoya and materials were obtained there in the growing season, but cultivated plants were also used. Hundreds of plants were examined during the years from 1949 to 1955. The anatomical studies were made usually from microtome serial sections, stained with safranin and fast green or with safranin and Delafield's haematoxylin.

**External morphology**

Fig. 1 shows the plant whose leaf tips have just emerged on the earth surface at the beginning of April. Several leaves (*f₁*, *f₂*, *f₃*) are found on the short axis produced from the top of the brown tuber densely covered with the root hairs. At the node of *f₁*, three absorbing roots are elongating horizontally. A decayed thin scale (*s₃*), brown in colour, embraces the base of the erect stem, concealing a small bud (*s₃b*), 1 mm in length, in its axil. Fig. 2 shows the subterranean parts of a plant in the middle of June. In the fertile plant, the erect stem is now somewhat elongated, and several absorbing roots, arising at the nodes of *f₁* and *f₂*, are longer and brown in colour, covered with root hairs. No lateral rootlets are produced. Besides the absorbing roots, one root-like organ, (*f₂b*) and soon later one more (*f₁b*)
appear respectively from the parts near the axils of $f_2$ and of $f_1$. In external view these organs, in this phase of development, can only be distinguishable from the absorbing root by their white colour and their lack of root hairs. The root-like organ, the young sinker continues the horizontal elongation until the flowering season (August), often exceeding lastly 10 cm in length. Then the tip turns downwards, coloured in brown (Figs. 4 and 5), and gradually increases its length and diameter, being covered with hairs (Fig. 6). Until the end of September, the brown part develops into a spherical tuber, 1 cm or less in diameter (Fig. 7). The tuber has a neck (Fig. 7, n), through which it is connected with the horizontal slender part (stalk) of the sinker. In November the aerial parts begin to die and all the subterranean organs, except the new tubers which remain alone through the winter, shrink and fall into decay sooner or later. Non-flowering plants also follow the same processes.

The plant just germinated from the seed is represented by a spherical protocorm as is usual with the Orchidaceae. Within a few months several foliar leaves are produced at the upper pole of the protocorm which increases its length and diameter gradually and develops into the first tuber covered with root hairs. The tuber has neither an apical meristem nor a root cap. The first absorbing root arises at the second node, and the first sinker primordium usually at the axil of the third or fourth leaf. The tuber derived directly from the protocorm dies without producing the flowering axis in the first year of germination.

Structure of the mature tuber

The main part of the full-grown tuber observed in Autumn (Figs. 7 and 13) is a typical tuberous root having a rudimental rootcap-like tissue (Fig. 13, c), starch

1) More accurately speaking, the parts slightly deviate laterally from the real axil or above it.
reserving fundamental tissue and monostele consisting of polyarch radial bundles. The neck encloses a terminal bud covered with a thin scale leaf (Fig. 13, s3) in its central cavity, which communicates with the outside through a small opening (m). The opening, located in a place 5-10 often 20 mm from the top of the neck, is so small that it is hardly visible to the naked eye, and its existence was not described by Ogura (1953); but sometimes marginal part of the opening protrudes slightly, thus the position of the opening is easily suggested. As shown by the semidiagrammatic transection through the neck (Fig. 12), the leaves f1, f2 and s3 within the neck have the axillary buds f1b, f2b and s3b respectively. These leaves and buds correspond to the respective organs indicated by the same symbols in Figs. 1 and 2. The scale leaf s3 is a few cell layers in thickness, no vascular tissue being observed except only in one example among hundreds of tubers studied. f1b and f2b are the primordia of the sinkers which elongate in the following growing season, while s3b remains undeveloped throughout and shares the fate of the mother tuber, dying usually in late autumn of the following year.

On one side of the neck, there is a tubular stele consisting of several collateral bundles (Figs. 12 and 14, bc). This is the stele of the sinker or stalk and bends at the base of the terminal bud and goes into it. The stele of the tuber (Fig. 13, rc) is separated from the curved part of the stalk stele. Figs. 8-11 show the transections through the distal part of the stalk shown in Fig. 13. s1t is a rudimental collateral bundle which is separated from the upper side of the stalk stele and comes to an end (Fig. 13, s1t) near the opening. This is a leaf trace belonging to the first leaf
on the sinker axis. A rudimental vascular strand $s_2$ (Figs. 11 and 13), observed in about half the plants studied by the writer, is regarded also as a leaf trace belonging to the second leaf, although it fades out at both ends.

In the older tuber, the rootcap-like tissue (root pocket) peels off completely and the tuber apex is also covered with the rhizoderm having root hairs.

**Development of the sinker**

In autumn, the axillary buds $s_{2b}$, $f_{1b}$ and $f_{2b}$ within the neck are initiated exogenously in an acropetal order, each as a cup-shaped process. The process develops to be 1 mm in length and then its development is suppressed until the following year. The bud in this stage (Fig. 15) has no peculiar features, the shoot apex being enclosed by the primordial leaves $s_1$ and $s_2$. In the coming late spring, $f_{2b}$ begins first to exhibit the elongating growth as a sinker by means of the rib meristem (Fig. 16, rm), which appears at the zone behind the node of $s_1$. However, the primordial leaves $s_1$ and $s_2$ scarcely grow further, consisting of a small number of immature cells. Two procambial strands, the one detached from the upper side of the sinker stele (Fig. 17, $s_{2t}$), the other from the lower side (Fig. 17, $s_{2t}$), are differentiated acropetally and the one goes into $s_1$, the other into $s_2$. Therefore, $s_1$ is undoubtedly an inverted prophyll and $s_{2t}$ is its leaf trace. $s_1$ and $s_2$ never produce their axillary buds even if in their last stages of development.

In a later stage of sinker elongation, a mass meristem (Fig. 17, mm) becomes differentiated from some periblem cells near the base of $s_{2t}$. The meristem consists of rather small cells rich in protoplasm; however, its outer boundary layer is not clearly distinguishable from the surrounding tissue. After the flowering season is over and the sinker is almost fully elongated, the distal lower halves of the horizontal sinker itself and of the primordial leaves exceed considerably the opposite halves in cell elongation. As the results the upward bending of the sinker axis
takes place (Fig. 18); $s_1$ and $s_2$ are prolonged on one side more remarkably than on the other side; the small procambial strand (Fig. 18, $s_{1t}$) is dissected from the sinker stele and the opening ($m$) is displaced towards less distal part of the sinker. Meanwhile, the cells between the epidermis and the meristem become vacuolated and a slit (Fig. 18, $cv$) appears between the epidermal and subepidermal layers. The protoderm and probably the calyptrogen are established from the outermost part of the meristem. The vacuolated cell group (Fig. 13, $c$) mentioned above covers the apical meristem firmly as if it were a root cap. Therefore, it is in reality a sort of root pocket, as the calyptrogen produces only a few cell layers. After the epidermis is destroyed a typical root covered with the root pocket becomes exposed as if it were a direct continuation of the sinker axis (Fig. 19). The part of the root structure is rapidly enlarged, being covered with the rhizoderm having root hairs on its surface, thus the root tuber is formed. It must be noticed that the differentiation of rhizoderm proceeds across the part of the root structure even to the subepidermal part of the neck. This results in the peculiar features of the neck: although the neck itself is not a root as its ontogeny shows, its surface layer is represented by the rhizoderm having root hairs after the epidermis is peeled off.

When the sinkers, $f_{1b}$ and $f_{2b}$, are artificially injured in the early stage of their development, $s_{3b}$ often develops into a sinker. Such compensatory development of the sinker has been described in other species of the Ophrydinae by Stojanow (1917), Ziegenspeck (1930), Sharman (1936) and others. Although the normal sinker produces no absorbing roots, the writer has often found the compensatory sinker, on which a single absorbing root arises at the base of the prophyllar trace $s_{3t}$ (Figs. 20 and 21). The development of such an absorbing root may be interpreted as the compensatory response to the injury of the normal absorbing roots rather than as a phenomenon confined to the compensatory sinker alone.

**Discussion**

It has been pointed out by some authors that the sinker of the Ophrydinae is nothing but a normal axillary bud in the early stage of its development. This holds true also in the case of *Pecteilis*. The sinker of *Pecteilis* is, however, elongated extraordinarily by means of the rib meristem situated immediately behind the first node; and then an adventitious root originates from the node of the second primordial leaf and becomes tuberous. A mass meristem, from which the main part
of the root is differentiated, is initiated in the periblem near the shoot apex, so it is of mesogenous origin rather than of exogenous, according to the terminology of Guttenberg (1940). Although the roots of the Ophrydinae were often described as of exogenous origin by some authors such as Stojanow (1917), Fuchs and Ziegen-speck (1925), and Burgeff (1932), they may also be of mesogenous, i.e. of the outer periblem origin.

The morphological nature of the sinker in the Ophrydinae has variously been interpreted (vid. Ogura, 1953). Ogura considered that the distal part of a sinker is a combined system of some roots, and the proximal part a combined system of cauline and radical characters. Thus he applied the term rhizophore to the latter part of the sinker. So far as the present study of Pecteilis concerns, it is quite certain that the proximal slender part (stalk) of the sinker is the hypopodium of an axillary shoot and of typical cauline nature, the distal tuberous part a single adventitious root originating from the second node. The morphological peculiarities are observed only in the part between the stalk and the tuber, i.e. in the neck. The ontogeny shows that the neck corresponds mainly to the parts between the first and the third nodes of a lateral shoot. Accompanied by the development of the adventitious root, the shoot apex itself falls into a cavity formed by the characteristic growth of those parts mentioned above. The rhizoderm differentiation which is usually confined to the root itself, proceeds to the subepidermal part of the neck across the part of root structure. The neck, accordingly, loses its epidermal layer and is covered with the rhizoderm having root hairs. Then we may call the neck a sort of the periclinal chimera consisting of the stem and root. If any special term is prepared, it should be applied to the neck alone. The cases, in which an organ other than the root is covered with rhizoderm, have been described (e.g., the cotyledonary petiole of some geophilous species in the Ranunculaceae, Berberidaceae and Umbelliferae—Haccius, 1953).

All the sinkers of fusiform, handform and tuberous types observed in many species of the Ophrydinae show one and the same fundamental construction derived from an axillary shoot accompanied by an adventitious root (Fig. 23). This holds true also in the case of the sinker of Pecteilis. Most of other species, however, differ from Pecteilis in the following respects: 1) the adventitious root is initiated
and grows at a very early stage of sinker development; 2) the hypopodium or the sinker does not elongate very long; 3) the rhizoderm differentiation is confined to the part of typical root nature.

The development of the sinker, which was treated by Ogura as of the stoloniferous type, will be described in the following paper.

**Summary**

In the early stage of development, the sinkers of *Pecteilis radiata* are typical lateral buds arising at the axils of the fourth and fifth leaves on one monopodium. In summer the hypopodium of the lateral bud is elongated extraordinarily by a rib meristem and is hardly distinguishable from the absorbing roots except by its white colour and the absence of root hairs. Then a mass meristem appears within the periblem near the second node, and later it develops into a tuber.

The full-grown sinker consists of three parts—the stalk, the neck and the tuber. The stalk corresponds to the hypopodium of a lateral shoot and is a typical cauline axis; the tuber, the distal part of the sinker, is a single adventitious root of the mesogenous origin. The calyptrogen is not so active that a root pocket derived from the periblem of the mother axis covers the tuber apex firmly as if it were a real root cap, but in the older tuber the root pocket is peeled off completely and the tuber apex is also covered with the rhizoderm having root hairs. The neck is represented by the connecting part between the stalk and the tuber, and morphological peculiarities are observed in this part alone. The neck has a central cavity, at the bottom of which the terminal bud of the lateral shoot is situated. The ontogeny shows that the neck is derived from the parts between the first and the third nodes of a lateral shoot by the characteristic growth of the parts. The rhizoderm is, however, differentiated not only at the part of typical root nature but also at the part of the neck, and then the epidermis of the neck is replaced by the rhizoderm after it is peeled off. Therefore, the neck may be said to be a sort of the periclinal chimera consisting of the stem and root.

**Literature cited**