ly activated by Ca ions flowing into the fibers during depolarization (*2*).

In sodium-containing solution, the flow of calcium ions into the fiber again is essential in order to obtain maximum activation of steady-state contraction, but this relation is not direct and instantaneous. In the potential range between the threshold for sodium current (−65 mv) and the threshold for calcium current (−30 mv), only a small steady-state contraction could be activated; and this did not depend much on the membrane potential. Beyond the threshold for I_{Ca}, the steady-state contraction increased gradually at each potential. This steady state was reached, however, only after five or six equal depolarizations, even though I_{Ca} was fully activated during the first depolarization. Maximum steady-state contractions were attained at about +20 mv. The time constants of activation of I_{Ca} and of activation of steady-state contractions were very different in sodium-containing solution, maximum activation being attained only with depolarizations lasting 200 to 300 msec (*4*).

During double-step voltage clamps (Fig. 1), the first step of depolarization (to −38 mv) activated only a small contraction if I_{Ca} was not previously switched on at V_2 (−33 mv). When I_{Ca} was fully activated at V_2, however, the steady-state contraction at V_1 was greatly increased and a second, smaller contraction was observed at V_2. In order for the positive inotropic response at V_1 to reach steady state, I_{Ca} had to flow at V_2 during five or six identical depolarizations. Moreover, if the clamp step V_2 was suddenly omitted (not shown in Fig. 1), the first depolarization to −38 mv still activated a large contraction; but this early contraction decreased to a much smaller value, within two or three depolarizations, to −38 mv.

These indirect effects of I_{Ca} on contraction in sodium-containing solution can best be explained if the flow of calcium ions into the fibers is assumed to fill intracellular stores from which calcium can be released by depolarizations below the threshold for I_{Ca}. Owing to the presumed partial depletion of these stores during each depolarization, steady-state levels within the stores are achieved only after I_{Ca} has been activated during five or six identical depolarizations. If these stores have not been filled previously by the flow of I_{Ca}, only a weak steady-state contraction can be activated. In contrast to the situation in sodium-free solution, direct activation of contraction by the flow of calcium ions seems to be only of minor importance in sodium-containing solution. These results could help to explain the recent observations by others of staircase phenomena and potentiation of contraction in mammalian cardiac muscle (*5*).

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Pistillate Papaya Flower: A Morphological Anomaly

Abstract. *The pistillate flower of* Carica papaya *is a pleurogynous unisexual form derived intraspecifically from a perigynous bisexual ancestor. It is a morphological anomaly in that the ovary consists of two cycles of carpels which, in the ancestor, arise on the receptacle at different levels as dissimilar orders of organs. The bulk of the pentamerous ovary and the dorsal carpellary vascular system are derived from a cycle of five stamens in the ancestor. The ventral carpellary system is inherited intact from the ancestor which has normal morphology in the sense that the carpels consist of a single cycle of sporophylls.*

The papaya (*Carica papaya* L.) is a polygamous species of large herbaceous dicotyledonous tropical plants (popularly called trees), cultivated for its edible melon-like fruit. Hermaphroditic trees are characterized by a form of bisexual flower known as "elongata" which has ten epipetalous stamens arranged in two cycles of five each. (Fig. 1A). Superficially, the upper cycle appears to lie opposite the lobes of the pentamerous sympetalous corolla and the lower cycle lies opposite the sinuses between the lobes. The ovary is su-

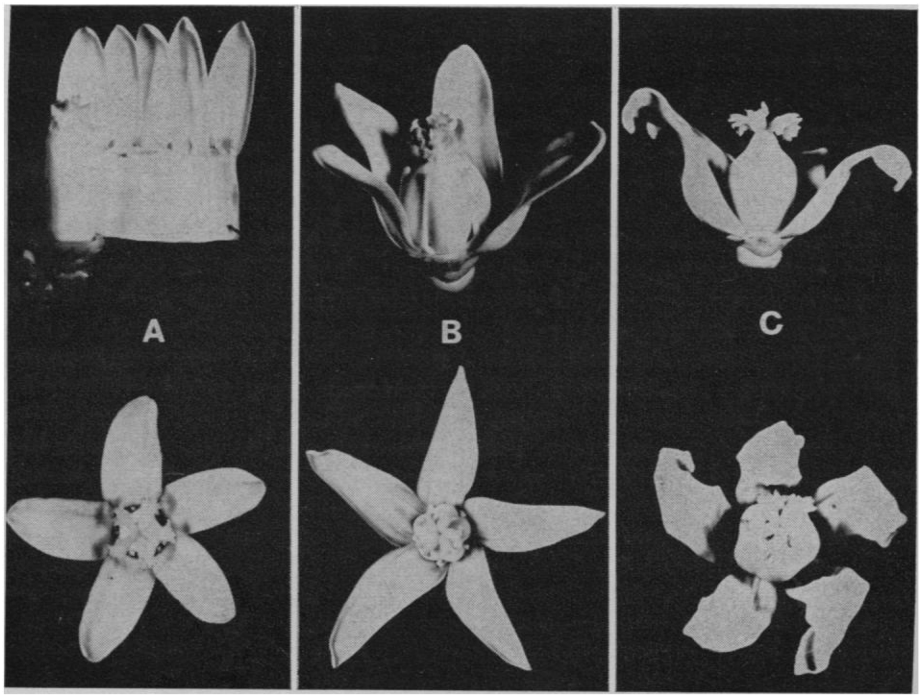
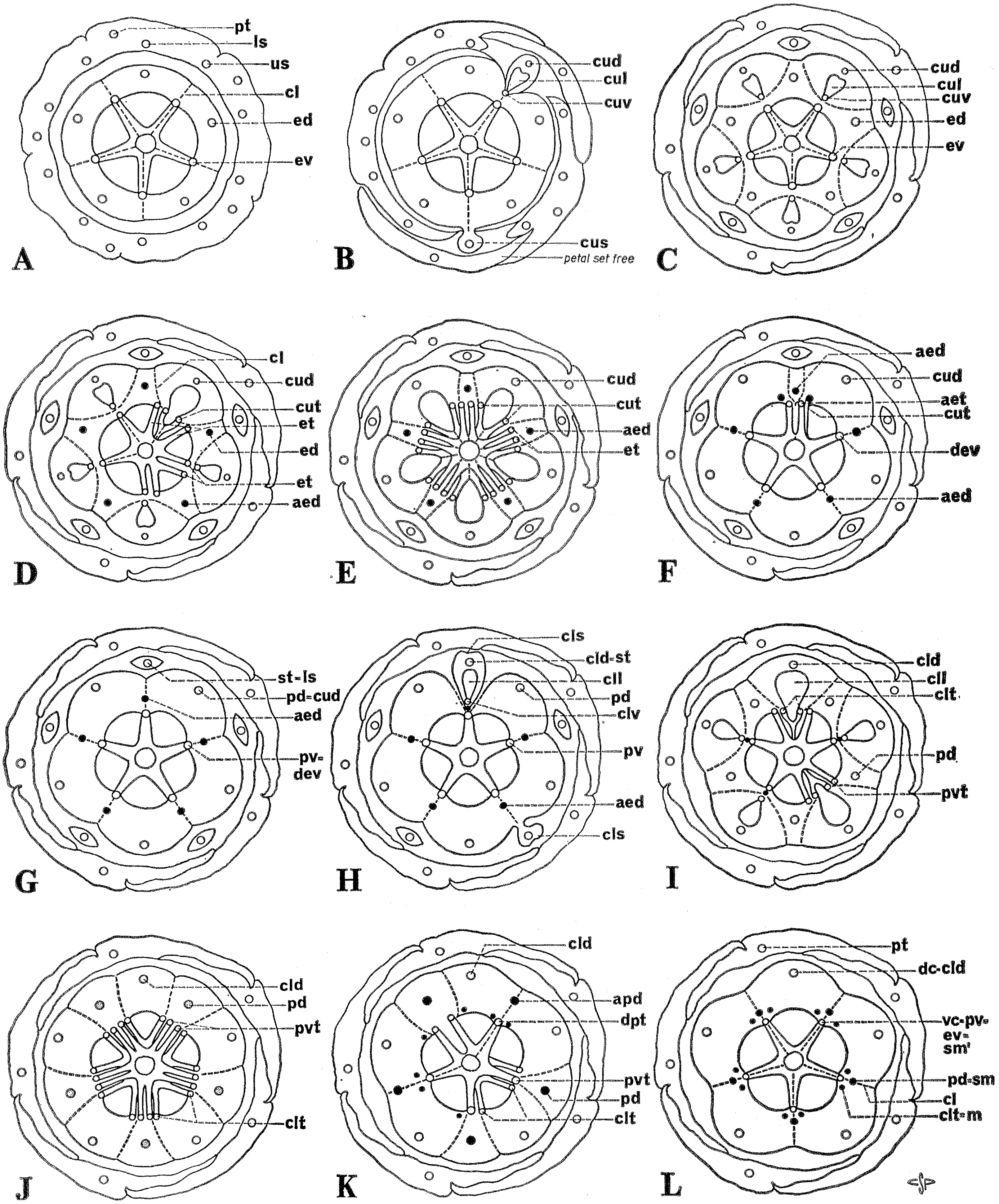


Fig. 1. Side and top views of papaya flower types. (A) Elongata, (B) pentandria, and (C) pistillate.

perior, cylindrical with slight furrowing, and five-carpellate with the lobes lying opposite the corolla sinuses. Hermaphroditic trees frequently bear another form of bisexual flower known as "pentandria" which has only five stamens, a sympetalous corolla with a greatly reduced tube, and a partially inferior ovoid, deeply furrowed five-carpellate ovary, with the lobes alternating with corolla sinuses (Fig. 1B). Pistillate trees are characterized by a monotypic form of unisexual flower having neither stamens nor vestiges of stamens (Fig. 1C). The flower is sympetalous, but the region of connation is so obscure that it has often been described as choripetalous. The ovary



is ovoid and five-carpellate with conspicuous dorsal lobes which lie opposite the corolla sinuses. The basal region of the ovary is adnate to the perianth tube, and, therefore, inferior in insertion on the receptacle.

Devi (*1*) described in detail the anatomy of the ovary of the pistillate flower in a study dealing with the vascular anatomy of flowers of species in the order Parietales. He erred, however, by describing the pistillate flower as having ". . . a superior ovary and a polypetalous corolla." He did discover a cycle of weak bundles, which had not been reported previously, arising on the same radial planes as the ventral carpellaries. He labeled them *SM*, stating, "There is little doubt that they are secondary marginal strands . . . these bundles do not furnish any ovular traces." Also, he discovered another set of bundles which he labeled *M*. Of these he wrote, "The latter bundles set off rather quickly, and immediately divide into two branches, each of which arranges itself on either side of the developing locule. They further split up into smaller branches which get consumed in supplying some of the first formed ovules." He interpreted the ventral carpellary bundles as second order secondary marginals, and labeled them *SM'*.

These extraneous bundles proved to be important clues in a study of papaya flower anatomy, furnishing explanations for certain conjectural morphological features of the pistillate flower. The explanations are to be found in an extraordinary intraspecific sequence of events involving both the androecium and the gynoecium in the derivation of a unisexual flower from a bisexual ancestor.

The elongata flower is the hypothetical ancestor from which two phylogenetic lines diverged intraspecifically, each terminating with derivation of a unisexual form. The staminate flower is the end product of one line, the pistillate flower the end product of the other line.

Derivation of the staminate flower proceeded along the classical line, that is, by phylogenetic loss of the gynoecium without appreciable disturbance either to structure or arrangement of other floral organs; consequently, it needs no further discussion. Derivation of the pistillate flower, however, represents a departure from classical theory.

According to classical theory, the unisexual flowers of the polygamous and dioecious species of angiosperms derive phylogenetically from bisexual forms by loss of function, reduction, or disappearance of the androecium or gynoecium (*2*). In some species, the nonfunctional organs persist externally as vestigial or rudimentary structures; in other species, they disappear entirely. Nevertheless, evidence of their former existence is present in the internal anatomy of the derived form as vestigial vascular traces originating on the stele of the receptacle in positions where one would expect them to be. Derivation of the pistillate papaya flower does not conform to classical theory (Fig. 2).

Sequential transitions in floral form providing evidence for the derivation of the unisexual pistillate flower from a bisexual ancestral form are found among the flowers of "sex-reversing" male and hermaphroditic trees. Frequently, the entire series (Fig. 3) can be found in one tree during a year. Much of the evidence is provided by carpellization of stamens, a commonly occurring, copiously documented phenomenon in papaya (*3*).

The sequence leading to derivation of the pistillate flower begins in the elongata flower (Fig. 2A), with stamens of the upper set becoming carpelloid and fusing with the ovary (Fig. 2B). Complete carpellization of the stamens with concomitant achievement of a functional condition gives rise to a form of pentandria flower in which the ovary has two whorls of carpels, an inner one with parietal placentation, and an outer one with

Fig. 2. Diagrams of transverse sections of papaya flowers showing intraspecific transitions in morphology between the ancestral elongata flower and the derived pistillate flower (sepals omitted). Broken lines in ventral bundles indicate that they are double bundles consisting of a trace to each of two abutting carpels. (A) Elongata, showing initial numbers and arrangement of parts; *pt*, petal trace; *ls*, lower stamen trace; *us*, upper stamen trace; *cl*, carpel limit; *ed*, dorsal carpellary bundle; *ev*, ventral carpellary bundle. (B) Teratological elongata, showing (at bottom) one upper stamen in an incipient stage of carpellody (*cus*) and adnation to the elongata ovary, and another more fully developed carpelloid stamen (at top), and corolla segments free in region of stamen carpellody; *cud*, dorsal bundle of carpelloid upper stamen; *cuv*, ventral bundle of carpelloid upper stamen; *cul*, carpelloid stamen locule. (C) Derived multiloculate pentandria, showing all five upper stamens carpellodic and adnate to the elongata ovary. (D) Multiloculate pentandria, showing (at top) opening of a carpellodic stamen locule into the cavity of the underlying elongata ovary, accompanied by separation of its carpellary bundle and the elongata ventral carpellary bundle into component traces; at bottom, separation elongata bundle traces belonging to an aborting carpel from those of abutting carpels; *aed*, dorsal carpellary bundle of aborting elongata carpel; *cl*, carpel limit; *cud*, dorsal trace of carpellodic upper stamen; *cut*, ventral trace of carpellodic upper stamen; *ed*, dorsal bundle of elongata carpel; *et*, ventral trace of elongata carpel. (E) Multiloculate pentandria, showing all upper carpellodic stamen locules opened into central elongata ovarian cavity, all elongata carpels aborting, and all 20 component ventral traces of the two cycles of carpels. (F) Multiloculate pentandria in penultimate stage of reduction, showing all but one completely abortive elongata carpel, and reorganization of the two traces of the same carpel into a new ventral bundle (*dev*). (G) Derived pentandria showing arrangement of parts, and primary vascular system; *st* = *ls*, stamen of pentandria flower, identical to lower stamen of elongata flower; *pd*, pentandria dorsal carpellary bundle, identical to the dorsal bundle of a carpellodic upper stamen; *pv* = *dev*, pentandria ventral carpellary bundle, identical with the new ventral bundle derived from the two ventral traces of an elongata carpel. (H) Teratological pentandria, showing initial stages of carpellody of lower cycle of stamens, comparable to B above; *cls*, carpelloid lower stamen; *cld* = *st*, dorsal carpellodic stamen bundle; *cll*, carpellodic stamen locule; *clv*, carpellodic stamen ventral bundle. (I) Initial pseudopistillate, showing all stamens of the pentandria flower carpelloid and adnate to the pentandria ovary, with two carpellodic stamens comparable to D, above. Locules beginning to open into the central cavity causing separation of their own ventral bundles and those of abutting carpels to separate into component traces; *lt*, carpelloid lower stamen trace; *pvt*, pentandria ventral carpellary trace. (J) Derived pseudopistillate, showing all carpellodic lower stamens opened into the central pentandria cavity, incipient abortion of the pentandria carpels, and all 20 component traces of the two cycles of carpels. (K) Pseudopistillate, showing reduction and realignment of traces resulting from abortion of pentandria carpels; *dpt*, derived double bundle consisting of two traces belonging to the same pentandria carpel. (L) Derived pistillate, showing arrangement of parts, and primary vascular system; *pt*, petal trace; *dc* = *cld*, dorsal carpellary bundle of pistillate ovary, identical to carpelloid lower stamen dorsal bundle; *vc* = *pv* = *ev* = *sm'* = *vc*, ventral carpellary bundle of pistillate ovary, identical to *pv*, the carpellary bundle of pentandria ovary, *ev*, the ventral carpellary bundle of the elongata ovary, and *sm'*, the second order submarginal traces of Devi (*1*); *pd* = *sm*, the vestigial dorsal carpellary bundle of the pentandria ovary, which is identical to Devi's submarginal bundle; *cl*, carpel limit; *clt* = *m*, vestigial carpelloid lower stamen trace, which is identical to Devi's marginal bundle.

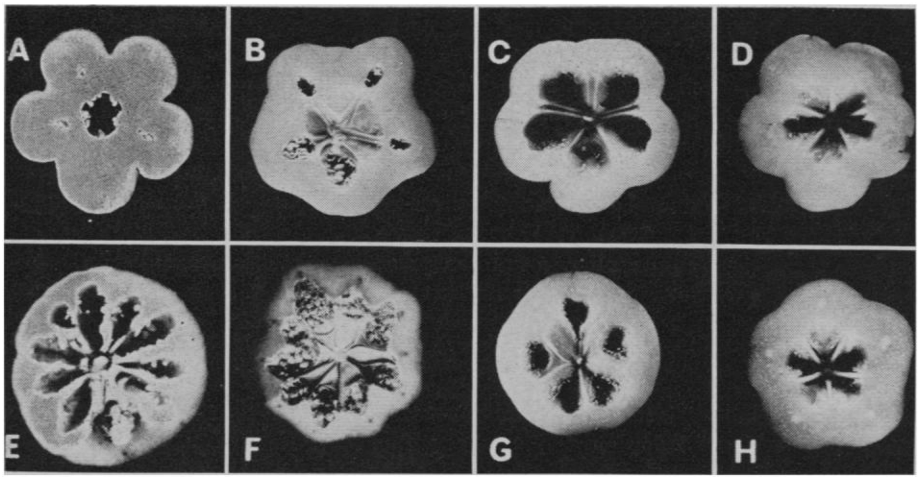


Fig. 3. Transections of papaya flower ovaries showing stages between carpellody of the upper cycle of stament of the elongata flower and the derived pistillate flower. (A) Multiloculate pentandria (see Fig. 2C). (B) Opening of carpellodic stamen locules into central cavity and reorientation of ventral carpellary traces (see Fig. 2D). (C) Penultimate stage in transition from multiloculate pentandria to typical pentandria (see Fig. 2F). (D) Derived pentandria (see Fig. 2G). (E) Carpellody of stamens and opened locules in pentandria (see Fig. 2J). (F) Reduction of pentandria and realignment of ventral traces (see Fig. 2K). (G) Penultimate stage in transition from pentandria to pistillate. (H) Derived pistillate (see Fig. 2L).

the locule of each carpel isolated from the others (Figs. 2C and 3A) and with axile placentation.

The next step is opening of the carpelloid stamen locules into the central cavity (Figs. 2D and 3B). This causes separation of each central carpellary bundle into its component traces, one for each of two abutting carpels. These traces are forced to migrate to new positions (Fig. 2, E and F; Fig. 3C). Complete opening is accompanied by abortion of all underlying elongata carpellary tissue excepting the ventral carpellary system which supplied the placenta, and the typical pentandria flower is derived (Figs. 2G and 3D). The dorsal carpellary bundles of the abortive elongata carpels persist as vestigial bundles in the pentandria flower, however (Fig. 2D; *aed*). The orientation of the dorsal lobes of the derived ovary is reversed in comparison with that of the elongata ovary with respect to the lobes of the corolla.

The pentandria flower is the start of the final steps in the sequence. The remaining stamens go through steps identical to those of the upper set, that is, carpellody, adnation to the ovary (Fig. 2H), opening of the locules (Fig. 2I), and forcing separation of the ventral carpellary bundles with consequent realignment of the component traces (Fig. 2, J and K; Fig. 3, E–G). Abortion of the pentandria pistil accomplishes derivation of the pistillate flower (Figs. 2L and 3H). The ventral carpellary system which supplies the placenta, as in the pentandria flower, is the persistant ventral system of the ancestral elongata flower. Evidence of the abortive pentandria pistil is present in the form of vestigial bundles in the derived form (Fig. 2L; *pd* = *sm*, *clt* = *m*). The dorsal lobes of the ovary are now oriented to the positions occupied by those of the elongata ovary with respect to the lobes of the corolla.

In view of events leading to derivation of the pistillate flower, Devi's *SM* bundles are vestiges of the dorsal carpellary bundles of the pentandria ovary which are derived from the three-trace bundles of the upper set of stamens. His *M* bundles are abortive ventral traces of the carpelloid lower set of stamens of which only the dorsal carpellaries (Fig. 2L; *dc* = *cld*) are functional. His *SM'* bundles are the surviving traces of the elongata ventral carpellary system inherited by the pistillate flower.

Derivation of the pistillate flower as hypothesized provides the following explanations for conjectural morphological features. (i) No stamens are recognizable because those of the upper set have aborted completely while those of lower set have become transmuted into sterile carpels comprising part of the pistillate flower pistil and have lost their identity as stamens. (ii) Vestigial traces of the upper stamens actually are present as extraneous bundles, however. These arise higher on the receptacle than do those of the dorsal carpellary lobes, whereas one ordinarily would expect to find them originating on the vascular cylinder below the dorsal carpellaries; inferior insertion results because the stamens which become the carpels of the pistillate flower are epipetalous. The term "pleurogyny" describes this kind of inferior insertion (*4*).

The hypothesis is supported by (i) progressive reduction in number of stamens from 10 to 0; (ii) structures in various stages of transmutation from typical stamens to typical carpels; (iii) progressive abortion of underlying carpels as new carpels develop from stamens or in positions normally occupied by stamens; (iv) splitting of ventral carpellary bundles, and migration and realignment of the component lateral traces; (v) reversal and reversal again of orientation of the lobes of the ovary in relation to other floral organs; (vi) change in insertion of pistil from superior to inferior; (vii) progressive reduction in length of androperianth tube from conspicuous to obscure sympetaly; (viii) presence of vestigial vascular traces to upper cycles of organs, now lost, in adaxial positions in the pistillate flower; and (ix) correlative change in shape of ovary from cylindrical in the elongata flower to ovoid in the pistillate flower.

The angiosperm flower is generally conceived as a determinate stem tip bearing appendages, which may be fertile, in the form of sporophylls or sterile in the form of sepals, petals, staminodes, and so forth. These appendages are homologous with leaves and, therefore, with each other. Any organ has the potentiality under proper genetic or physiological stimulus to assume the form and function of another. The literature is replete with documentation of this point. Why, then, cannot the pistillate flower represent a form in which a set of appendages that would have been stamens in a bisexual form have developed into carpels instead, with coincidental loss of the original pistil and remaining stamens? This would account for carpels occupying the positions of stamens. This supposition fails to account for the various disparities between the elongata flower and the pistillate flower and for the unique situation in which a carpel consists of tissues derived from two different cycles of appendages.

The ovule-bearing organs of a typical flower, the carpels or megasporophylls, make up the gynoecium, which may range in number from many to one, in arrangement from spiral to whorled, and in morphology from simple to complex. Nevertheless, insofar as known, each carpel is a complete unit derived from a single sporophyll with a self-contained vascular system consisting most commonly of a dorsal carpellary bundle and two ventral carpellary bundles. The pistillate papaya carpel does not conform to the concept of development from a single sporophyll.

Unisexual flowers resulting from transmutation of stamens into carpels or carpels into stamens have been reported in many species of plants (*5*). Generally, such flowers have been regarded as abnormal or teratological forms resulting from the influence of external factors upon the physiology of the plant and as having no real evolutionary significance.

In the derivation of the pistillate papaya flower, however, sterile carpelloid stamens have replaced fertile stamens and become part of the ovary with retention of epipetaly. The flower is visualized as an interesting morphological anomaly, therefore, with the greater part of its ovary consisting of sterile carpels and its ventral vascular system inherited without modification from a previously existing whorl of carpels farther up on the receptacle. Evidence of several intervening cycles of organs between the dorsal and ventral vascular systems which disappeared phylogenetically persists in the form of vestigial traces in the internal anatomy of the ovary. The morphological structure described has become fixed genetically in the pistillate papaya tree. Unlike hermaphroditic trees among which sex reversal in response to physiological influences is commonplace, the pistillate tree is virtually unknown to undergo any change of sex.

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Shark Pit Organs: Response to Chemicals

Abstract. *Nerve fibers from pit organs and canal neuromasts are distinguished by the nature of their electrophysiological response to mechanical and chemical stimulation. Pit organs respond to touch but have a relatively high threshold compared with canal neuromasts. They respond readily to sodium and potassium chloride solutions, the rate of discharge increasing with the concentration of the solution. Order of effectiveness with 1 molar solutions of monovalent cations is as follows: potassium, rubidium > sodium, ammonium > cesium, lithium. Anions are ineffective. Divalent cations such as calcium and magnesium are inhibitory. Responses to acid, sugar, and quinine are either very slight or inhibitory.*

Two hypotheses regarding the function of pit organs (Fig. 1) in sharks are that (i) they serve as external taste buds (*1*) and (ii) they are free neuromasts serving as mechanoreceptors for mediating water displacements (*2*). With electrophysiological techniques, we have studied the responses of pit organs to acid, sugar, quinine, mechanical stimulation, and solutions of monovalent cations.

Small nurse sharks (*Ginglymostoma cirratum*) (40 to 70 cm) shipped from Florida to Hawaii were used because this species can survive for several hours on the operating table. Sharks were secured to boards and covered, except for the head and tail, by gauze irrigated with seawater. During all experiments, seawater containing 0.02 g of anesthesia (MS222) per liter was introduced into the mouth by way of a plastic mouthpiece and was allowed to flow out the opercula.

Activity was recorded from the lateralis nerve where it approaches the dermis on the caudal peduncle. This nerve receives fibers from canal neuromasts of the lateral line and from a row of pit organs along the dorsolateral margin of the caudal fin (*3*). The nerve was exposed and cut, and the end of the posterior segment was separated into small bundles which were looped over a silver-wire electrode (*4*). The nerve response was recorded on a tape recorder through a conventional RC coupled high-gain amplifier, and later displayed on an oscilloscope screen and photographed if necessary. Recordings were also made from the external mandibular nerve which receives fibers from the mandibluar canal and mandibular row of pit organs on the lateral and ventral surface of the head (*2*). In all, recordings were made of 76 pit organ fibers in 29 sharks.

Fibers from canal organs were distinguished from those from pit organs by the nature of the response. The former responded readily with increased discharge rate to light touch on the denticles of the skin, whereas the pit organ fibers had a higher threshold, responding only to pressure on them. Although both showed spontaneous activity, the spikes were relatively larger in the pit organ fibers (about 1 to 3 mv) than in the canal organ fibers (less than 1 mv) and the activity was maintained for a longer period of time (2 or 3 hours as compared to ½ hour). When the tail area was flooded with seawater or salt solutions, the discharge rate of the canal organ fiber did not change.

Table 1. Effectiveness of various 1*M* salt solutions on the pit organ. Spike number in 5 seconds of the response plateau shown by: +++, more than 70; ++, between 70 and 40; and +, less than 40.

Sodium salts	Spike No.	Chloride salts	Spike No.
NaCl	++	NaCl	++
$NaNO_3$	++	KCl	+++
$NaHCO_3$	+	LiCl	+
Na_2SO_4	++	RbCl	+++
Na-glutamate	++	CsCl	+
Na-propionate	++	NH_4Cl	++
$NaCH_3SO_4$	+	Choline-Cl	—
$NaC_2H_5SO_4$	+		