Abstract

The floral vascular anatomy and floral morphology of Pleea tenuifolia Michx., a south-eastern coastal plain endemic, are reported, and compared to its Englerian tribal cohorts, Tofieldia and Narthecium. In Pleea, an ensheathing bract and a three-parted, basally connate bracteole, both vascularized, are associated with each flower. Fusion bundles are not characteristic of the tepal, stamineal, and gynoecial vascularization. From a pedicel with an 18-bundled, cross-sectional, ring configuration, the floral parts are supplied by bundles of simple division. Basally each tepal receives three traces. Nine stamens with simple bundles are typical—six in the outer whorl, three in the inner whorl. The dorsals share a common basal bundle with the outer tepal median, whereas the ventral’s common basal bundle is shared with the outer stamen bundles and the outer tepal laterals. The axial ventrals directly supply the ovules via horizontal funicular traces. Several gynoecial features are significant. An intercarpellary gland formed within the upper pedicel opens externally and cuts off three, vascularized stipitate carpels. These three carpels are not fused laterally, only appressed via interdigitating papillae. In fruit, the carpels separate septicidally. The seeds are appendaged. Because of the extensive, reported similarities between Pleea tenuifolia and the genus Tofieldia, the former is transferred to the genus Tofieldia.

Introduction

The monotypic genus Pleea of L. C. Richard published by Michaux (1803) precedes Pleea of Persoon (1805). The only species in the genus, P. tenuifolia (rush featherling, star flower), has had a long taxonomic
Fig. 1.—Distribution map of *Tofieldia tenuifolia* (Michx.) Utech based on examined and cited herbarium specimens (solid dots), and county records (open circles) mapped by Johnson (1969) and also based on herbarium specimens.

history as a coastal plain endemic (Wells, 1967; Small, 1933; Johnson, 1969; Radford et al., 1964). Though rare in the eastern United States, it is plentiful within its limited areas of occurrence on the southern, outer Coastal Plains (Fig. 1). It flowers in autumn, and occurs in pine-land swamps, grassy bogs, savannahs, and pocosins. The sites are usually open with acid soil. The shallow spreading rhizome system results in a close scattering of clones.

Beginning with Redouté’s illustration (t. 25), which accompanied the type description (Michaux, 1803), several additional illustrations of *Pleca tenuifolia* have been presented (Redouté, 1808; Sims, 1818; Lamark, 1823; Small, 1933; Radford et al., 1964). Redouté’s first illustration (t. 25) in Michaux (1803) is the same as that presented later in the massive *Liliacées* (Redouté, 1808; t. 456). The Lamark illustration (1823) is a modified version of the first Redouté illustration. Sims (1818)
used original material for his *Botanical Magazine* illustration (t. 1956). The floral line drawing in Small (1933) has inaccuracies.

Botanists in the past have expressed varying opinions on the relationship of *Pleea*. Richard (Michaux, 1803) noted a relationship to *Narthecium*, whereas Asa Gray (1836) indicated an affinity towards *Tofieldia* and *Zygaenadens*. Both Engler (1888) and Krause (1930) have placed *Pleea* in a similarly circumscribed tribe, the Tofieldieae, which contains *Tofieldia* Hudson and *Narthecium* L. Hutchinson (1934, 1959), on the other hand, has used a larger tribe, the Narthecieae, to circumscribe *Pleea*, *Tofieldia*, *Narthecium*, and several other genera. The exact relationship of *Pleea* to *Tofieldia* and *Narthecium*, as well as the other genera of Hutchinson’s Narthecieae, has not been adequately documented.

Gates (1918), while relating *Pleea* to *Tofieldia* (including the segregate genus *Triantha* (Nutt.) Baker) and *Narthecium*, makes a direct comparison with inferred relatedness to *Tofieldia* (*Triantha*). The major floral differences between *Pleea* and *Tofieldia* (*Triantha*) according to Gates (1918) are the lack of the three-parted connate pedicel bracteoles in *Pleea*, the outer subtending bract in *Pleea* is large and spathe-like, the stamen number in *Pleea* is higher, that is, nine to 12 in *Pleea* versus six for *Tofieldia* (*Triantha*), and the versatile anthers in *Pleea* are elongated.

This study is part of a continuing series of investigations on the primitive members of the Liliaceae (Utech and Kawano, 1978; Utech, 1978a, 1978b) and will present the floral vascular anatomy and morphology of *Pleea tenuifolia*. Particular detail will be given to the stamen number and morphology, which has historically isolated this species, as well as to the bracts and bracteoles of the raceme. A comparison to the other members of the Englerian Tofieldieae, that is, *Tofieldia* and *Narthecium*, will be made and evidence will be presented, which shows that *Pleea* should be considered a member of the genus *Tofieldia*.

**Materials and Methods**

Collections of *Pleea tenuifolia* were made from two populations in North Carolina: Onslow Co., SW of Holly Ridge along US 17, pine savannah, (Utech 77-513 CM), and Pender Co., 4.0 mi NE of Hampstead on US 17, savannah, (Utech 77-515 CM). Flowering inflorescences were fixed in 3:1 (absolute ethanol: glacial acetic acid) for 10 h with subsequent storage in 70% ethanol. Standarized paraffin sections were cut between 14–16 μ and stained in safranin-methylene blue (Johansen, 1940; Sass, 1958). A total of 30 flowers of *P. tenuifolia* were sectioned, 15 from both populations. As an additional check on these serial sections, whole flowers were cleared and stained in a NaOH-1% fuchsin mixture (Fuchs, 1963).

The specimens used for the distribution map (Fig. 1) are cited at the end of the paper following Holmgren and Keuken (1974). Figs. 3–5 are composite photomicrographs which present the vascular floral anatomy of *P. tenuifolia*, whereas Figs. 6–9 are line-
Fig. 2.—Illustration of Tofieldia tenuifolia (Michx.) Utech. A) Habit showing basal equitant leaves, fibrous root system, and simple scape. B) Flowering scape with three open flowers. C) Same scape as B with flowers and buds omitted to show the large,
drawn summary diagrams. No teleological implications are intended by the descriptive manner of vasculature presentation and discussion. The various bundles and traces are letter-coded for ease in comparison. This coding parallels that used in our previous liliaceous studies (Utech and Kawano, 1975, 1976a, 1976b, 1976c, 1978; Utech, 1978a, 1978b). For comparison Figs. 10-11 present past illustrated cross-sections of *Tofieldia* (Anderson, 1940; El-Hamidi, 1952). The cross-sections of *Narthecium americanum* (Fig. 12) are from our unpublished data (Utech, unpublished manuscript). Following this vascular presentation, a tribal and generic taxonomic discussion will be presented, which concludes in the formal transfer of *Pleea tenuifolia* to the genus *Tofieldia*.

**Observations**

*Inflorescence, Pedicels, Bracts, and Bracteoles*

The fertile individuals of this rigid, subscapose perennial herb are usually (3.5)-5.5-7.0-(8.0) cm tall from a basal rosette of stiff, linear, equitant leaves. The larger leaves average 22.5 cm long (range: 15.0-30.0 cm) by 1.7 mm wide (range: 0.90-2.5 mm). The leaves are aristate tipped. Progressively smaller leaves occur upwards on the lower half of the scape.

The simple, terminal bractose raceme of *Pleea tenuifolia* usually has five to eight flowers, which are confined to the upper one-fourth of the total plant’s height. The raceme has an interrupted appearance due to a series of large, green, erect, spathe-like bracts which ensheath the pedicels of each flower. The bracts have numerous parallel veins, decrease in size upwards and are marked with a prominent aristate tip (Fig. 2). The bract proper at a given node is consistently longer than its associated aristate tip. The average length of the lower three bracts is 2.3 cm (range: 1.1-2.8 cm), whereas the average length of its associated tip is 1.2 cm (range: 0.4-2.0 cm). Upwards there is a progressive decrease in bract length. A given bract is imbricated around the pedicel of the flower at that node, as well as the base of another bract that contains the pedicel of the flower for the node above. The total pedicel length of a given flower can only be observed by removing the ensheathing bract (Fig. 2).

The total pedicel length is slightly greater than that of the bract proper and slightly shorter than the total bract length. The average pedicel length for the three lowest flowers is 3.0 cm (range: 2.4-4.5 cm). When the bract is removed, a basally connate whorl of three bracteoles is observed near the middle to the upper one-third of the ensheathing bracts. D) Enlarged bract from mid-scape, prominent aristate tip. E) Pedicel and three-parted, basally connate bracteoles, both are normally hidden by the ensheathing bract. F) Enlarged flower showing the nine stamen configuration and the three free styles. G) Distally appendaged seed. H) Floral diagram that includes the bract and the bracteoles. (Scale indicated; drawing by Ms. Pamela J. Leopold)
Fig. 3.—Cross-sectional series from *Tofieldia tenuifolia* (Michx.) Utech showing the vascularization of the pedicel and bracteole. A) Pedicel section below the level of bracteole formation; alternating bundles within the central ring establish outwardly the bracteole bundles and inwardly the pedicel supply; a sclerenchymatous sheath is associated with the vascular ring; the cells of the pith are differentiated from those of the cortex (40×). B) Slightly oblique section above A and showing both the basally connate bracteoles (B) and the partially freed pedicel (25×). C) Section above B; the central pedicel with its 18-bundled vascular ring is surrounded by the three, free, marginally imbricated bracteoles (B₁–B₃) (25×). D) Upper pedicel above the bracteoles; a sclerenchymatous sheath surrounds the vascular ring, as in A, and separates the undifferentiated cortex from the central pith (30×). E) Upper pedicel below the receptacle; the intercarpellary
pedicel (Fig. 2). These three-parted pedicel bracteoles are normally hidden by the ensheathing outer bract. The bracteoles are usually 1.0–1.5 cm long from their fused base to the ends of their freed tips (Fig. 2).

Below the three-parted bracteoles, the pedicel is circular in cross-section. At this level, the pedicel vascularization usually consists of a closely spaced ring of 18 bundles (Fig. 3A). Both the fruiting and flowering pedicels have a sclerenchymatous sheath around these bundles. The cells of the pith differ from those in the surrounding cortex, and it is within the former that the open, intercarpellary gland (Gl) is formed (Figs. 3; 6 D–E; 7 D–E).

The pedicel vascularization above and below the insertion of the basally connate bracteoles is the same (Figs. 3 A–D; 6 A–C; 7 A–C). Below the level of bracteole attachment, a bundle is formed via division from each of the 18 pedicel bundles. These 18 derived bundles depart outward on alternating radii from the parental pedicel bundles. The connate bracteoles form a tube in lower cross-sections. At their mid-length they are subdivided into three free segments (Fig. 3 C). Basally each segment is associated with six of the 18 derived bundles (Figs. 6 A–D; 7 A–D). Not all of the six bundles per segment continue to the bracteole tips.

The joint occurrence of both bracts and bracteoles in Pleea is significant in a comparison between Pleea and Tofieldia. Vascular and morphological attention has been given to the bracteoles because they have frequently been omitted in past species descriptions. This "apparent" lack has been used in part for the taxonomic isolation of Pleea. Both Johnson (1969) and Radford et al. (1964) correctly reported the three connate bracteoles in Pleea, whereas Kunth (1843) noted two bracteoles, and Baker (1879) noted one to two bracteoles. Others reported none. Gates (1918), for example, stressed the "unobserved" absence of the bracteoles in Pleea as a difference between Pleea and Tofieldia (Triantha).

A survey of the species of Tofieldia shows a whole series of bract-bracteole combinations and reductions. Most species clearly have both, though in no case does a species of Tofieldia have a bract, which approaches the shape and size of that in Pleea. Frequently the shape and the size of the bracteoles in Tofieldia are similar to those in Pleea. The location of the bracteoles in Tofieldia, however, is normally directly below the flower, and appears as a second calyx (calyculus).
Fig. 4.—Outer and inner tepal and stamen vascularization in *Tofieldia tenuifolia* (Michx.) Utech. A) Cross-section at the level of freed tepals and stamens, as well as the carpellary stipes; a typical pair of outer stamens (OS₁ and OS₂) are between an outer tepal (OT) and the gynoecium, which has a dorsal (D) indicated (40×). B) Longitudinal section cut peripherally and perpendicular to an outer supply radius; in the upper area, two outer stamen (OS₁ and OS₂) bundles are divergently departing, whereas in the lower area, the clustered outer tepal supply occurs, that is, the OTM and the OTL pair (40×). C) Cross-section showing the typical outer tepal-stamen vascularization; section below that in A, and through the midreceptacle; the intercarpellary gland is prominent; the typical pair of outer stamen (OS₁ and OS₂) bundles is along the same radii as the outer tepal laterals.
Tepals and Their Vascularization

The linear to linear-lanceolate tepals of the two whorls are distinct and subequal. The three outer tepals are slightly wider than those of the inner cycle. The outer tepals have an average length of 1.5 cm (range: 1.0–1.7 cm) and an average width of 3.2 mm (range: 2.5–4.0 mm), whereas the inner tepals have an average length of 1.5 cm (range: 0.9–1.6 cm) and an average width of 2.7 mm (range: 2.0–3.7 mm). In flower the inner tepal surfaces are a whitish yellow centrally and dull green along the margins. The outer tepal surface is a dull yellowish white. The tepals persist into the fruiting stage and undergo a color change to a brown. There is no tepal perigyny within either cycle. There is however a limited degree of stamen epitepaly (Figs. 2, 6, 7).

Basally each tepal receives three bundles—two laterals and a median. The outer tepal vasculature is established as three division bundles move outwards. Each is derived directly from a single pedicel ring bundle. The two bundles, which determine the outer tepal laterals (OTL), each undergo two successive divisions. These additional divisions establish besides the outer tepal laterals (OTL), the outer stamen traces (OS), and the ventral supply (V) (Figs. 6 D–H; 7 D–H; 8; 9). The pedicel ring bundle, which establishes via a division the outer tepal median (OTM), on the other hand, normally undergoes a single division, which results in the formation of the outer tepal median (OTM) and the dorsal (D) (Figs. 4 A, C–E; 6 D–H; 7 D–H; 8; 9). If there were two divisions in this later parental pedicel bundle, an additional stamen trace would be formed, thus giving a stamen number greater then the typical nine (Figs. 4 D; 9).

The origin of the inner tepal vasculature is similar to that observed for the outer tepals (Figs. 4 B, E–F; 8; 9). Basally each inner tepal receives two laterals (ITL) and a median (ITM). The two laterals per tepal arise directly from bundles in the pedicel ring and do not undergo any receptacle division (Figs. 4 E–F; 8). The bundle, which supplies the inner tepal median, on the other hand, does undergo a single di-

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(OTL), whereas the outer tepal median (OTM) shares a common radius with the dorsal (D) (50×). D) Cross-section showing the atypical outer tepal-stamen vascularization; section level similar to C, but from a different flower; three outer stamen (OS₁–OS₃) bundles are associated with the three outer tepal bundles; a dorsal (D) indicated; the additional outer stamen (OS₂), which is along the OTM-D radius contributes to the greater than nine total stamen configuration (50×). E) Cross-section showing the typical inner tepal-stamen vascularization; the branch bundle that becomes the inner stamen (IS) trace is along the same radius as the inner tepal median (ITM); two inner tepal laterals (ITL) are present (50×). F) Longitudinal section cut peripherally and perpendicular to an inner supply radius; the inner stamen (IS) bundle is in the same vertical plane as the inner tepal median (ITM) (35×).
vision, and the resulting innermost product of this division functions directly as the inner stamen trace (IS) (Fig. 4F).

Occasionally, there are additional laminal divisions within the tepal laterals. These divisions involve both the outer tepal laterals (OTL) and the inner tepal laterals (ITL), and result in five veins (traces) within the tepals. When this condition occurs, the higher vein numbers are usually observed only near the base of the freed tepals. The veins are parallel within the laminal tepal surface of both whorls, and there is no cross-connection between them.

**Stamen Number, Morphology, and Vascularization**

The stamen number of nine for *Pleeea* has historically been used to isolate this monotypic genus from the typical six stamen lilies. Within the artificial Linnean system, *Pleeea* was placed in the Enneandria (nine stamens) class and the Trigynia order (Michaux, 1803; Sims, 1818). Redouté’s illustration (t. 25), which accompanied the type description (Michaux, 1803), shows three open flowers each with nine stamens. Sims’ illustration (t. 1956) for Curtis’ Botanical Magazine (1818) shows two open flowers with 10 stamens each, and adds that “the stamens are by no means confined to the number nine, but seems to vary from six to twelve. The laciniae of the corolla are constantly six, perhaps, therefore the number twelve may be the most natural for the stamens, though most generally reduced below that number by abortion.” This was the first report of a stamen number other than nine for *Pleeea*.

Endlicher (1840) stated that the stamen number was nine with a pair of stamens in front of each outer tepal, that is, *ante sepala exteriora gemina*. Both Kunth (1843) and Baker (1879) reported the stamen number as varying between nine and 12, whereas Engler (1888) and Krause (1930), on the other hand, stated that the stamen number varied between six and 12, but that the total stamen number was usually nine with a pair of stamens in front of each outer tepal.

A stamen count of 200 flowers from 47 different individuals (herbarium specimens) selected from throughout the range gave the following stamen number distribution: six—0; seven—0; eight—0; nine—189 (94.5%); 11—0; 12—0. Of the 30 flowers embedded and sectioned for anatomical examination, 28 had nine stamens and two had 10 stamens. Clearly the lower numbered stamen classes, that is six through eight, are rare or nonexistent, as are the higher numbered stamen classes, that is, 11 and 12.

In the normal nine stamen flowers (Fig. 2), the original observations of Endlicher (1840) were confirmed. There are two stamens in front of each outer tepal and a single stamen in front of each inner tepal. This configuration gives a total of nine stamens. When a tenth stamen is present, it is associated with an outer tepal and the pair of stamens
already present. There are three stamens in front of one outer tepal, two stamens in front of two outer tepals and a single stamen in front of each of the three inner tepals, which gives the total of 10 stamens. Theoretically, it would be possible to have 12 stamens arranged in the following fashion—three stamens associated with each outer tepal (nine) and a single stamen associated with each inner tepal (three). An inaccurate sketch of a *Pleeea* flower with 12 stamens was presented by Small (1933). It shows a partial floral sketch with a single stamen in front of an outer tepal, a single stamen in front of an inner tepal and a single stamen between the outer and inner tepal.

The stamens of both the outer whorl and the inner whorl are equal. Both whorls are freed directly within a short vertical distance from the gynoecial base, although there is a limited degree of stamen adnation to both tepal whorls. The glabrous filaments are dilated basally, filiform terminally, and divergent at anthesis. Each filament contains a single vein (trace). The average free filament length for the filaments from both whors is 4.45 mm (range: 4.2–5.2 mm). The three anthers of the two whors are equal, basally divided, laterally dehiscent, and versatile. The average anther length is 2.69 mm (range: 2.4–3.0 mm). Each anther sac is bilocular and the walls of the endothelial cells are lined with banded thickenings.

The vascularization of the outer stamens differs from that of the inner stamens. The outer stamen vascularization is associated with the bundles supplying the outer tepal laterals of the outer tepals. Each pedicel ring bundle, which branched to form an outer tepal lateral (OTL), continues vertically for a short distance and then divides. The outermost division product becomes the outer stamen trace (OS) (Figs. 4 A–C; 6 E–H; 7 E–H; 8; 9). The two pedicel bundles, which supply the two outer tepal laterals (OTL), also supply the two outer stamen (OS) traces.

The single inner stamen (IS) trace is derived from the continuing bundle that remains following the formation of the inner tepal median (ITM) (Figs. 4 E–F; 6 E–F; 7 E–F; 8; 9). The three single inner stamen traces of the flower are therefore along the inner tepal median (ITM)—septal radii. Each of the outer stamens (OS) within the three outer pairs, on the other hand, is 30° from the outer tepal median (OMM)—dorsal (D) radii. Summary diagrams show the patterns of stamen vascularization (Figs. 6–9) for the typical nine stamen configuration.

The derivation of the tenth (or additional) stamen is from the outer tepal median supplying bundle, and not as one might guess from the inner tepal vasculature. The tenth (or additional stamen) is derived from an additional division and departing branch from the bundle, which supplies both the outer tepal median (OTM) and the dorsal (D) (Figs. 4 D; 9 A). The net result is three stamens associated with the
Fig. 5.—Serial cross-sections through the gynoecium of Tofieldia tenuifolia (Michx.) Utech. A) Tepals and stamens cut off from the gynoecium; the central intercarpellary gland is broadly six armed; the three larger arms are along the septal radii, whereas the three smaller arms are along the dorsal (D) radii (25×). B) Section above A in which a stipitate carpel is freed via the external connections along the septal radii of the intercarpellary gland; dorsal (D) and ventrals (V) indicated (30×). C) Similar section to B, but emphasis is on the smaller, dorsal radius arm; dorsal (D) and ventrals (V) indicated (30×). D) Stipitate carpel section above C showing the internal locular (Loc) opening; the cells of the locular wall differ from those which line the intercarpellary gland; dorsal (D) and two ventrals (V) indicated (30×). E) Section through the mid-gynoecium; within the locule (Loc) there are two horizontally orientated ovules (ov), one of which clearly shows the bitegmic condition; the two ventrals (V) of the carpel are located along the inrolled septal wing tips (40×). F) Upper gynoecium showing the interdigitating papillae of the stigmatoidal support system along the septal radii; ventral (V) supplies for two locules (Loc) indicated (40×).
outer tepal. One is along the OTM-D radius, this is the additional one, and there are two typical stamens each located ca. 15° on either side of the OTM-D radius. In the 30 sectioned flowers, there was never an indication of additional stamen vasculature associated with or derived from bundles supplying the inner tepal laterals (ITL).

The pattern of stamen and tepal vascularization in Pleea parallels that in Tofieldia, but not Narthecium. An examination of several species of Tofieldia (T. calyculata (L.) Wahlenb., T. racemosa (Walt.) BSP, T. glabra Nutt., T. coccinea J. Rich., T. japonica Miq., T. glutinosa (Michx.) Pers.) indicates a reduction series in this genus for the number of tepal bundles. Two examples are provided in Fig. 9 (C–D) for Tofieldia, while sketches A and B are for the 10 (or additional) stamen and nine stamen configurations, respectively. This sequence does not directly imply a phylogenetic arrangement of Pleea and members of Tofieldia, but rather an anatomical reduction series relating the outer tepal and outer stamen vasculature. A similar type of pedicel ring configuration occurs in both Pleea and Tofieldia, as well as a similar type of division within these bundles to form the various types of tepal and stamen traces.

Three outer stamens is the rule within the genus Tofieldia. However there is a reduction series in the number of veins (bundles) in the outer tepals. Three veins (Fig. 9 C) is the most common type, but outer tepals with a single median also occur (Fig. 9 D). The pattern in Tofieldia with three outer tepal bundles and a single outer stamen (Fig. 9 C) is identical to the pattern of the inner tepal and stamen in Pleea (Figs. 4 E–F; 6 E–H; 7 E–H; 8).

In the genus Narthecium there are consistently six stamens, and the outer and inner stamen bundles have a fusion origin which is totally unlike that observed in Pleea and Tofieldia (Utech, unpublished manuscript). The bundles are also bifid throughout most of the filament length. Both Pleea and Tofieldia have 2-sulcate pollen grains, whereas those in Narthecium are 1-sulcate (Erdtman, 1966).

Gynoecium Morphology and Vascularization

The obovoid to elliptic, tricarpellate gynoecium in Pleea exhibits several primitive liliaceous characteristics. Basally the three carpels are free and have vascularized stipes (Figs. 5 B–D; 6 H–J; 7 H–J). This stipitate region is associated with an intercarpellary gland that originates in the upper pedicel’s pith. Because the outer adjoining septal surfaces are only appressed with papillae that interdigitate, there is no carpel fusion throughout the vertical height of the gynoecium. In fruit the leathery carpel walls show no indications of true dehiscence, though most floras indicate septicidal dehiscence. Actually the carpels do separate along the septal radii, but this is due to pulling apart of
Fig. 6.—Serial cross-sections of *Tofieldia tenuifolia* (Michx.) Utech. A) Lower pedicel below the bracteoles with a ring of 18 vascular bundles, this section as well as B and C are surrounded by the bract. B) Mid-pedicel showing the connate bracteole with a 18-bundled vascular configuration, the pedicel also has a 18-bundled configuration. C) Upper pedicel with 18 bundles surrounded by the three freed bracteole blades, each blade has a reduced number, four, of bundles. D) Upper pedicel below the receptacle, three of the 18 bundles depart along the yet undefined dorsal radii, triwedged cavity in the center is the opening of the intercarpellary gland, gland lined with secretory cells. E) Receptacle base with the intercarpellary gland exhibiting six wedges, that is, the three larger along the septal radii and the three smaller along the dorsal radii; 12 of the 18
the interdigitating papillae along the septal walls. The style and stigma of each carpel are free.

The intercarpellary gland (Gl) in *Pleea* originates as an irregular cavity in the central pith region of the upper pedicel (Figs. 3 E–F; 6 H–I; 7 H–I). From the base of this cavity, it is lined by a single layer of intercarpellary papillae. The papillloid cells stain darker than those in the surrounding pith and probably have a secretory function (nectary). The gland cavity enlarges further up the floral axis; first along the three, yet undefined septal radii, and then along the dorsal radii (Figs. 3 F; 5 A; 6 D–G; 7 D–G). The gland is six armed, at this receptacular level. As the tepals and stamens are freed, the bases of the three carpels are also freed along the gland’s septal radii, creating the freed stipes of the three carpels. Also at this level, the intercarpellary papillae extend along the septal radii of the periphery of each carpel. The level of gland opening is below the level at which the locules open. The gland’s external opening is continuous with the three septal grooves that continue up the sides of the gynoecium.

In *Pleea*, the basal stipes of each freed carpel have three bundles—a dorsal (D) and two ventrals (V) (Figs. 5 B–D; 6 H–I; 7 H–I). The epidermis of the stipes is differentiated from the septal and central

original bundles have divided and their branch bundles are along shared radii, nine of the 12 divided bundles, that is, three sets of six bundles will with further division and orientation establish the dorsal and ventral vasculature, as well as the supply for the six outer stamens and the outer tepals, where the remaining three of 12 divided bundles, that is, three bundle pairs will establish the three inner stamens and the supply of the inner tepals. F) Receptacle base showing further bundle division and movement; three sets of three bundles have moved inwards to establish dorsal and two ventraals per set, the tepal medians of both the outer and inner whorls are established, as are the inner tepal laterals, the bundles lateral to the outer tepal medians are dividing to form the two outer tepal laterals and the two outer stamen bundles; intercarpellary gland increases in internal area. G) Outer tepals with three traces and the outer paired stamens cut off from the receptacle, the outer stamen traces have a shared origin with the outer tepal laterals; the inner tepals, also with three traces, and the unpaired inner stamen are not yet cut off. H) All tepals and stamens freed from receptacle-gynoecium; the nine stamen condition is typical; additional divisions have occurred within the outer tepals; three stipitate carpels are formed as the intercarpellary gland is freed to the outside along the septal radii, each carpel has a dorsal flanked by two laterals; the intercarpellary gland is lined with secretory cells at this level. I) Three stipitate carpels with locules and positioned vasculature; the stamens and tepals not shown; a second cell type replaces the secretory cells along the central floral axis. J) Midcarpellary section showing the interdigitating papillae along the septal wings, the septal wings are not fused; ovule supply occurs at this level, but ovules are not indicated; a unilocular relationship exists between the three carpels. K–M) Transition from the upper carpellary zone to the three freed styles; the three dorsals terminate slightly below the stigmas; a hollow pollen path lined with papillloid-stigmatoidal cells coincides with the central floral axis.
Tofieldia tenuifolia (Michx.) Utech

(= Pleea tenuifolia Michx.)

Fig. 7.—Projected cross-sections of Tofieldia tenuifolia (Michx.) Utech. Lettered sections correspond to those in Fig. 6.
facies which consist of papilloid cells. Along the central (inner) facies of the stipes, there are internal gland indentations along the dorsal radii, but these indentations are not basally connected with the locules of the carpels. There is no basal connection between the intercarpellary gland (Gl) and the locules (Loc). The locules (Loc) appear centrally within the broadening stipes.

Above the stipe region, a more elongated type of papilloid cell occurs along the central axis and the outer surfaces of the septal wings. This second type of papilloid cell replaces those that are characteristic of the basal intercarpellary gland (Gl). The locules (Loc) open at this level along the dorsal radii and the central axis. The three locules are subsequently confluent. The resulting compound gynoecium is therefore unilocular from a region just above the stipes, though the degree of lateral “fusion” of the adjoining septal wings is limited to the appressed, interdigitating papillae.

Fig. 8.—Longitudinal summary roll-out diagram of *Tofieldia tenuifolia* (Michx.) Utech showing the vascularization of the three basally connate bracteoles, the tepals and stamens, and the gynoecium. The following, text introduced, code applies to the various bundles: OTL = outer tepal lateral, OTM = outer tepal median, ITL = inner tepal lateral, ITM = inner tepal median, OS = outer stamen, IS = inner stamen, D = dorsal, V = ventral, and F = funicular trace. Only one set of the outer and the inner tepals have their vasculature labeled.
The inner septal wing tips are recurved (inrolled) into the locules. Each wing tip has a single ventral (V), which is reversed, that is, the phloem is adaxial and the xylem is abaxial, and this bundle reversal is associated with the septal tip being inrolled. From each ventral (V), a vertical series of funicular (F) branches arise (Figs. 4 E; 6 I–L; 7 I–L). There are usually 18 bitegmic ovules associated with each ventral (V) (Fig. 8), or 36 ovules per carpel. Terminally there is no cross-connection between the dorsal (D) and ventral (V) supplies.

There is no abrupt transition from the upper gynoecial regions to the three free styles (Figs. 6 L–M; 7 L–M). Papillae line the open central axis of the upper gynoecium and these papillae are also continuous along the adaxial stylar surface. The dorsals (D) are presented in the styles, the ventrals are not. Throughout the ovary, there is no branching of the dorsals. Also there are no septal axials in Pleea. Raphides were not observed.

The ovules in *Pleea* are bitegmic with their long embryo sac axes in a horizontal plane, and parallel to the dorsal radii (Fig. 5 F). The ovule orientation is best described as pleurotropous (terminology after Björnstad, 1970). The micropyles are directed towards the central axis and the open, intercarpellar papillae. There are two rows of ovules per carpel with each row supplied from different sides of the inrolled carpel margins. There are usually 18 ovules per row, that is, 36 ovules per carpel (Fig. 8). The funicular traces (F) and their stalk are also parallel to the dorsal radii, because lengthwise fusion has occurred between the funicular stalk and the adjacent outer integument. A short, distal appendage in the horizontal plane occurs at the chalazal end of each ovule. The appendage length increases following anthesis.

The brown, glabrous seeds are distally appended (Fig. 2). The clear appendage is thin and elongate (1.7–2.5 mm) and is attached at a slight angle to the seed proper. The seed is usually between 1.1 to 1.5 mm long. The horizontal seed packing is similar to that of the ovules. The seed appendages from one vertical carpellary row are directed horizontally into the locular space on the other side of the carpel. The appendages from the other vertical carpellary row are directed in criss-cross fashion to the opposite side of the locale. The criss-crossed appendages of the two seed rows can be seen in cleared mature fruits. The seed appendages in *Pleea*, as well as the packing of the seeds, are similar to those in many species of *Tofieldia* (Gleason, 1952; Hitchcock, 1944; Ohwi, 1965; Kitamura et al., 1965).

The independent stipitate carpels, the basal intercarpellary gland, and the lack of septal wall fusion, which characterize the gynoecial morphology of *Pleea*, are distinctive characters within the primitive subfamily Melanthioideae, but are not exclusively observed in *Pleea*. Similar carpel morphology and vascular anatomy occur in the genus
Fig. 9.—Comparative reduction series in Tofieldia diagrammed to show the different vascularization configurations within the outer tepals and outer stamens. Below each inset figure, there is a summary code: OS = outer stamen, OTL = outer tepal lateral, OTM = outer tepal median, D = dorsal, and V = ventral. A) T. tenuifolia with three outer tepal bundles and three outer stamen bundles; this outer configuration results in the rare 10, 11 or 12 total stamen number; cf. Fig. 4 D. B) T. tenuifolia with three outer tepal bundles and two outer stamen bundles; the latter share a common origin with the outer tepal laterals; this outer pattern results in the typical nine stamen configuration; cf. Figs. 2 F, H; 4 B–C; 6–8. C) Representative example, T. racemosa with three outer tepal bundles and a single outer stamen bundle; cf. Fig. 10; if the continuing dorsal (D) and the two ventrals (V) were excluded, this pattern would approximate that of the inner tepals and inner stamens of T. tenuifolia. D) Representative example, T. calyculata with a single outer tepal bundle and a single outer stamen bundle; cf. Fig. 11, and Leinfellner (1962a, 1962b, 1963) for additional reductions.
Table 1.—Generic comparison of the Englerian Tofieldieae: Pleea, Tofieldia and Narthecium.

<table>
<thead>
<tr>
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</thead>
<tbody>
<tr>
<td>Distribution</td>
<td>Southeastern U.S.; coastal plain; cf. Fig. 1</td>
<td>North temperate and circumpolar zones with outliers in the mts. of South America</td>
<td>East and west U.S.; Europe; East Asia; highly disjunct within temperate zone</td>
</tr>
<tr>
<td>Number of species</td>
<td>1; this paper</td>
<td>ca. 15–20; highly variable</td>
<td>ca. 4–5; very similar</td>
</tr>
<tr>
<td>Habit</td>
<td>Rhizomatous perennial with equitant leaves</td>
<td>Rhizomatous perennial with equitant leaves</td>
<td>Rhizomatous perennial with two-ranked leaves</td>
</tr>
<tr>
<td>Inflorescence</td>
<td>Simple raceme, few flowered, one flower per node</td>
<td>Simple to compound raceme, few to many flowered, one to three flowers per node</td>
<td>Simple, dense raceme, many flowered</td>
</tr>
<tr>
<td>Bract</td>
<td>Yes; large, ensheathing, aristate tipped</td>
<td>Yes; size variable</td>
<td>Yes; small, linear</td>
</tr>
<tr>
<td>Bracteoles</td>
<td>Yes; three-parted, basally connate, cf. Fig. 2</td>
<td>Yes and no; some groups with and some without; if present, three-parted</td>
<td>Yes; small, linear</td>
</tr>
<tr>
<td>Tepal vascularization</td>
<td>Constantly three-bundled</td>
<td>One to three bundled</td>
<td>Constantly three-bundled</td>
</tr>
<tr>
<td>Outer cycle of three</td>
<td>One; simple, single branch bundle</td>
<td>One; simple, single branch bundle</td>
<td>One; fusion product</td>
</tr>
<tr>
<td>OTM</td>
<td>Two; simple, single branch bundles</td>
<td>Zero to two; if present, then simple, single branch bundles</td>
<td>Two; simple, single radial branch bundles</td>
</tr>
<tr>
<td>OTL</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>-----------------------------------------------</td>
<td>--------------------------------------------------</td>
<td>--------------------------------------------------</td>
<td>--------------------------------------------------</td>
</tr>
<tr>
<td>Inner cycle of three</td>
<td>Constantly three-bundled</td>
<td>One to three bundled</td>
<td>Constantly three-bundled</td>
</tr>
<tr>
<td>ITM</td>
<td>One; simple, single branch bundle</td>
<td>One; simple, single branch bundle</td>
<td>One; fusion product</td>
</tr>
<tr>
<td>ITL</td>
<td>Two; simple, single branch bundles; cf. Figs. 6-9</td>
<td>Zero to two; if present, then simple, single branch bundles; cf. Figs. 10-11</td>
<td>Two; simple, single radial branch bundles; cf. Fig. 12</td>
</tr>
<tr>
<td>Pedicel vascularization</td>
<td>c. 18 ring bundles; cells of cortex unlike pith; surrounding sclerenchymatous sheath present; cf. Figs. 6-9</td>
<td>c. 18 ring bundles; cells of cortex unlike pith; surrounding sclerenchymatous sheath present; cf. Figs. 10-11</td>
<td>Three- and 12-bundled configurations; cells of cortex similar to pith; surrounding sclerenchymatous sheath absent</td>
</tr>
<tr>
<td>Intercarpellar gland (GI)</td>
<td>Yes; basal origin in pedicel; nectiferous; cf. Figs. 6-9</td>
<td>Yes; basal origin in pedicel nectiferous; cf. Figs. 10-11</td>
<td>No; cf. Fig. 12</td>
</tr>
<tr>
<td>Stamen number, vascularization and morphology</td>
<td>Usually nine; rarely 10 or more</td>
<td>Usually six, but variable (cf. Leinfellner, 1962a, 1962b, 1963)</td>
<td>Usually six</td>
</tr>
<tr>
<td>OS and IS</td>
<td>Simple, single branch bundle; cf. Figs. 6-9</td>
<td>Simple, single branch bundle; cf. Figs. 10-11</td>
<td>Bifid, fusion product; cf. Fig. 12</td>
</tr>
<tr>
<td>Anthers</td>
<td>Introrse, versatile, laterally dehiscent</td>
<td>Introrse, versatile, laterally dehiscent</td>
<td>Introrse, versatile, laterally dehiscent</td>
</tr>
<tr>
<td>Filaments</td>
<td>Dilated basally, glabrous; cf. Figs. 6-9</td>
<td>Dilated basally, glabrous; cf. Figs. 10-11</td>
<td>Ovoid basally, pubescent; cf. Fig. 12</td>
</tr>
</tbody>
</table>
### Table 1.—(Continued)

<table>
<thead>
<tr>
<th>Character</th>
<th>Genus 1</th>
<th>Genus 2</th>
<th>Genus 3</th>
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</thead>
<tbody>
<tr>
<td></td>
<td><em>Plea</em></td>
<td><em>Tofieldia</em></td>
<td><em>Narthecium</em></td>
</tr>
<tr>
<td>Carpel vascularization</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dorsal</td>
<td>Simple, single branch bundle</td>
<td>Simple, single branch bundle</td>
<td>Fusion product</td>
</tr>
<tr>
<td>Ventral</td>
<td>Simple vertical with many horizontally derived funicular branches; cf. Figs. 6–9</td>
<td>Simple vertical with many horizontally derived funicular branches; cf. Figs. 10–11</td>
<td>Numerous vertically parallel ventrals each with a one to one funicular correspondence; cf. Fig. 12</td>
</tr>
<tr>
<td>Carpel morphology</td>
<td>Ovary stipitate, basally apocarpous</td>
<td>Ovary stipitate, basally apocarpous</td>
<td>Ovary non-stipitate, sessile; basal placenta massive</td>
</tr>
<tr>
<td></td>
<td>Septal wing tips free and loculicidally inrolled</td>
<td>Septal wing tips free and loculicidally inrolled</td>
<td>Septal wing tips fused basally, free upper ovary and not inrolled</td>
</tr>
<tr>
<td></td>
<td>Septicidally separated; cf. Figs. 6–9</td>
<td>Septicidally separated; cf. Figs. 10–11</td>
<td>Dorsal grooves present; loculicidally dehiscent</td>
</tr>
<tr>
<td>Seed morphology</td>
<td>Distally appendaged seeds; cf. Fig. 2</td>
<td>Distally appendaged seeds</td>
<td>Distally and proximally appendaged seeds</td>
</tr>
</tbody>
</table>
Tofieldia (Figs. 10–11; Anderson, 1940; El-Hamidi, 1952; Table 1). These characters on the other hand are not found in the genus Narthecium (Fig. 12; Table 1; Utech, unpublished manuscript). Tofieldia and Narthecium are tribal (Tofieldieae) cohorts with Pleea.

**Summary**

Immediately following this summary of the vascular floral anatomy and carpel morphology of Pleea tenuifolia is a discussion and table (Table 1), which compares these aspects of Pleea to those in both Tofieldia and Narthecium.

The inflorescence of Pleea is a simple raceme with three to eight flowers. An elongate ensheathing bract with an aristate tip is associated with each pedicel. Basally the pedicel has an axial system of 18 bundles which are continuous to the base of the receptacle. At midpedicel length, a three lobed, basally connate bracteole tube is observed. Although 18 bundles enter the connate base, only several reach the three freed subsections.

Each of the 18 pedicel bundles contributes a branch bundle to the tepal supply. Nine are associated both in the outer and inner tepal whorls. Each of the three outer tepals has an outer tepal median (OTM) and two adjoining laterals (OTL). Likewise, each of the three inner tepals has an inner tepal median (ITM) and two laterals (ITL).

The usual stamen number is nine with two outer stamens per each outer tepal (six) and a single inner stamen per each inner tepal (three). The bundles for the outer stamens (OS) are derived via branches from the same pedicel ring bundles which established the outer tepal laterals (OTL). If an additional stamen were present, for example a tenth, it would occur through a division of the pedicel ring bundle that established the outer tepal median (OTM). The three inner stamens (OS) are derived from those pedicel bundles which established the three inner tepal medians (ITM).

The remaining portions of those pedicel ring bundles, which supplied the outer tepals (OTL + OTM + OTL) and the outer stamens (OS), establish the gynoecial vasculature. Three independent stipes characterize the base of the tricarpellate gynoecium in Pleea. Each stipe has three bundles, a dorsal (D) and two ventrals (V). The dorsal (D) is continuous via previous divisions at lower levels with the outer tepal median and their shared common pedicel bundle. The two ventrals (V) per stipe are continuous at a lower level with the supplies of the outer tepal laterals (OTL) and the outer stamens traces (OS) and the associated pedicel bundles.

The two ventrals (V) of each carpel have funicular branches (F) from each side of the locule. Therefore, there are two rows of ovules per
locule. There is no interconnection between the dorsal and ventral supplies. Only the dorsals occur in the stylar regions.

**Discussion and Concluding Remarks**

The present study has established several previously unknown facts about the carpel morphology of *Pleea tenuifolia*. At the level at which the tepals and stamens are freed, the gynoecium base is divided into three vascularized stipes. Free stipitate carpels are rare in the Liliaceae *sensu lato* (Gates, 1918; Eames, 1961; Anderson, 1940; Brown, 1938). Stipitate carpels are, however, known in *Tofieldia*. Anderson (1940) presented both cross-sectional and longitudinal views of the basal stipes of *Tofieldia racemosa* (Fig. 10 B, E), whereas a complete series of cross-sections for *T. calyculata* by El-Hamidi (1952) shows the basal origins of the stipes (Fig. 11 K–N). Additional personal observations of *T. glutinosa*, *T. glabra*, *T. coccinea*, and *T. japonica* have confirmed the presence of stipes throughout the genus. The morphology and vascularization of the stipitate carpels in *Tofieldia* are identical to those reported here for *Pleea* (Figs. 5 B–D; 6; 7). There are no stipitate carpel bases in *Narthecium* (Fig. 12; Table 1).

In *Pleea*, there is an intercarpellary gland which originates centrally in the upper pedicel, and extends upwards between the freed stipes. This gland is lined with differentially stained papillae which probably function as secretory cells for the basal (nectary) gland. Basal carpellar glands (nectaries) are extremely rare in the Liliaceae (Eames, 1931, 1961; Anderson, 1940), and are only known in *Tofieldia* (Fig. 10, Anderson, 1940; Fig. 11, El-Hamidi, 1952). There are no basal intercarpellary glands in *Narthecium* (Fig. 12; Table 1).

There are two other kinds of nectaries, which are prevalent in the Liliaceae *sensu lato*, but only one of them involves a gynoecial modification. These two types of functional nectaries are the tepal nectary and the septal (gland) nectary. The former is simply a basal, saccate tepal modification lined with secretory cells that serves directly as a nectary (Anderson, 1940; Utech and Kawano, 1976b, *Disporum sessile*; Utech and Kawano, 1978 *Heloniopsis orientalis*). The septal (gland) nectary, on the other hand, is formed by the incomplete lateral fusion of the outer septal wings (Anderson, 1940; Grassmann, 1884; Engler, 1888; Eames, 1931, 1961; Utech and Kawano, 1976a, *Maianthemum*; Utech, unpublished manuscript, *Smilacina*, *Polygonatum*). These nectaries are in the septal planes and their depth depends on the degree of septal wing fusion. The inner walls of these nectaries, that is, the lateral surfaces of the unfused septal wings, are lined with secretory cells, and usually have terminal openings in the upper carpellar stylar regions.

Although these two kinds of nectaries are common within the Lili-
Fig. 10. — Cross-sections (A–D) and a longitudinal (E) view of *Tofieldia racemosa* (Walt.) BSP, redrawn from Anderson (1940; Plates VIa and VIII). A) Receptacle base showing the continuous, three-armed intercarpellary gland below the base of the stipitate carpels; the outer tepals with three bundles each and the inner tepals with a single bundle; common gynoecial bundle per carpel (25×). B) Intercarpellary gland opening externally and subdividing the three carpels basally (apocarpous); stamens freed (25×). C) Disappearance of intercarpellary gland prior to locule opening; common gynoecial bundle of each carpellar stipe divides to form carpel supply (25×). D) Midgynoeicum section showing inrolled septal wing tips (25×). E) Longitudinal section which shows the relationship between the basal intercarpellary gland, the hollow central axis, and the vertical plane through the appressed septum and opposing locule (30×). Number code: 1, Three outer tepal traces (OTL plus OTM plus OTL). 2, Single inner tepal trace (ITM). 3, Single inner stamen trace (IS). 4, Continuous basal intercarpellary gland lined with nectiferous cells. 5, Common stipitate carpel bundle. 6, External gland opening. 7, Ventral pair. 8, Dorsal. 9, Septal groove and radius of appressed septal margins. 10, Unilocular, intercarpellary space around the floral axis. 11, Septum (dotted lines). 12, Septal groove is continuous with the lower intercarpellary gland. 13, External gland opening and carpellar stipe zone. 14, Basal origin of intercarpellary gland.

aceae, usually they are mutually exclusive within a given species, that is, a given species may have one or the other type, but never both. Furthermore, the tepal and septal glands are characteristic of certain subfamilial and tribal associations (Anderson, 1940; Grassmann, 1884),
Fig. 11.—Serial cross-sections of *Tofieldia calyculata* (L.) Wahlenb. redrawn from El-Hamidi (1952; Fig. 1). A) Stigma with terminal stigmatoidal tissue (35×). B) Stigma-style transition with stigmatoidal tissue lining the stylar opening (35×). C) Upper style showing the hollow stylar canal; dotted line indicates the appressed inner septal margins; no vasculature present (35×). D) Lower style with a dorsal and two ventrals; inner septal margins appressed (35×). E) Upper gynoecium showing three free styles; the inner septal margins of each carpel inrolled into the upper locular space (30×). F) Similar to E, but from a lower section; the outer septal margins are appressed laterally (30×). G) Similar to F, but from a lower section; centrally the three carpels are free along the floral axis, that is, the gynoecium is unilocular; dotted lines indicate laterally appressed outer septal margins, whereas the inner septal margins are inrolled (30×). H) Upper gynoecium showing the upper ovule tier; inward ventral rotation corresponds to the inrolling of the inner septal margins (30×). I) Midgynoecium, similar to H (30×). J) Midgynoecium, similar to I (30×). K) Lower gynoecium with both the inner and outer septal margins appressed; section below level of ovule attachment; the two carpel ventrals are simple and ascend vertically with numerous horizontal funicular traces derived from them (30×). L) Opening of the three locules from within, this precedes both the lateral appression of the outer septal margins and the inrolling of the inner freed septal tips (30×). M) Three apocarpous stipes of the three carpels are due to the external openings of the intercarpellary gland; each stipe has a dorsal and two ventrals; tepals and stamens omitted (30×). N) Slightly oblique cross-section through the upper recep-
and express a common phylogenetic background. The joint occurrence in Pleea and Tofieldia of the rare basal intercarpellary (gland) nectary is therefore most significant.

In Pleea the three carpels are never fused along the vertical septal planes (Figs. 6, 7). Interdigitating papillae line these appressed facies, but there is never any septal fusion. The free inner sepal tips (placenta) of each carpel are inrolled into the locules. The gynoecium is therefore unilocular, because one locule is confluent with the other. Identical carpellary modifications were reported for Tofieldia racemosa (Anderson, 1940; Fig. 10) and T. calyculata (El-Hamidi, 1942; cf. Fig. 11; Klotsch, 1846; Leinfellner, 1962a, 1962b, 1963). In fruit, the carpels of both Tofieldia and Pleea are separated along the appressed, papillae-lined septal facies in a type of septicidal dehiscence. Normal septicidal dehiscence implies a fusion along the sepal.

On the other hand, in Narthecium (Fig. 12, Table 1; Utech, unpublished manuscript) a totally different carpellary structure exists. The lateral septal facies are completely fused throughout their vertical height. There are no septal (nectaries) glands. The septal wing tips (placenta) are large, not inrolled and fused basally. Dorsal grooves are associated with a carpellary weakened zone that in fruit results in loculicidal dehiscence.

Floral variability for the European Tofieldia calyculata was reported in detail by Leinfellner (1962a, 1962b, 1963). Variation in the number, morphology, and vasculature of the bracteoles, three bracteoles forming a calyculus are typical, the tepals, the stamens, and the carpels were illustrated and statistically recorded. Tepal to stamen, as well as stamen to carpel (gynostamen), transitional intermediates were discussed. That such variation occurs in T. calyculata further suggests that unreported homologous variation (Vavilov, 1951) occurs elsewhere within the genus, and that the atypical, but stabilized stamen number of nine presented here for Pleea may not be as unusual as first thought.

The allopatric pattern of range replacement between Pleea and Tofieldia along the southern Atlantic Coastal Plain is noteworthy. Neither T. racemosa (Walter) BSP nor T. glabra Nuttall, which occur in the same general area (Johnson, 1969; Radford et al., 1964) as Pleea, occupy the same sites. Narthecium americanum Ker. is rare and found only in the pine barrens of the middle Atlantic Coastal Plain, and...
Fig. 12.—Cross-sectional series of *Narthecium americanum* Ker. from the New Jersey pine-barrens (Utech 76-890 CM). A) Lower pedicel with the six-bundled configuration; solid outer bundles will establish the outer tepal medians (25×). B) Midpedicel with the 12-bundled configuration; a pair of branch bundles depart from each of the three compound inner bundles; each branch bundle is also compound (25×). C) Upper pedicel with further subdivision of the inner three bundles and the formation of a fusion bundle between each; the fusion bundles will establish the inner tepal medians (25×). D) Pedicel-receptacle transition zone with six central axial bundles and three fusion dorsals along the same radii as the outer tepal medians; an outer tepal lateral adjoins each median, as well as a pair of branch bundles which establishes the outer stamen supply (25×). E) Receptacle base with six large axial bundles, the three dorsals, and three new fusion bundles along the septal radii; the outer tepals peripherally defined (25×). F) Pedicel-receptacle base enlarged from section D, but with the same number of bundles (25×). G) Level of locular opening; epitepal and staminal adnation occur within the outer cycles; a set of fusion bundles is formed between each pair of axial bundles along the dorsal radii within the central placenta (25×). H) Freed tepal and stamen cycles; paired bundles in each pubescent filament; two sets of fusion bundles present in the placenta, one set formed along the septal radii, the other along the dorsal radii; solid massive central placenta with obturators (25×). I) Midgynoecium with the central placenta loculicidally divided and lined with stigmatoidal cells; compound ventrals subdivided into isolated ventrals which have a one to one correspondence with an associated funicular trace (25×). J) Upper unilocular gynoecium; ventrals remain for upper ovule tier supply (25×). K) Upper gynoecium-style transition with only the three dorsals present; stigmatoidal cells line the laterally fused, but reduced septal margins (25×). L) Style with three dorsals and opposing dorsal grooves; stigmatoidal cells line the hollow stylar canal (25×).
southward in the Blue Ridge Mountains of North Carolina (Small, 1924; Radford et al., 1964; Johnson, 1969). A parallel range shift from the northern pine barrens to the southern mountains also occurs within two other primitive lilies—*Xerophyllum asphodeloides* (L.) Nuttall (Wood, 1971; Utech, 1978a), and *Helonias bullata* L. (Utech, 1978b).

If the genus *Tofieldia* is viewed broadly, as it currently is, and the morphological and vascular variations in bracts, bracteoles and floral parts seen as homologous series of reductions, then *Pleea tenuifolia* must be considered a species of *Tofieldia*.

**Taxonomic Consideration**

*Tofieldia tenuifolia* (Michaux) Utech, *comb. nov.*


Type presumably at Paris, but not seen. Description is such that no other species could have been meant. Type locality is wet forest margins in lower Carolina.

Rigid, subscapose, perennial herbs with stout rhizomes occurring in clumped clones. Leaves mostly basal, erect, evergreen, equitant, 1.0–3.5–(4.0) dm long, 1.5–4.0–(5.0) mm wide, bases auriculate, tips acute. Scapes stiff, (3.5)–5.5–7.0–(8.0) dm tall, with two to four leaves which are reduced upwards. Inflorescence a simple raceme with three to eight flowers; raceme interrupted by spathe-like, ensheathing bracts, bracts 1.1–2.8 cm long, reduced upwards, aristate tipped, 0.4–2.0 cm long. Bract ensheaths pedicel and a three-part bracteole, which is connate basally. Flowers perfect. Tepals linear to linear-lanceolate, free, three-nerved, persistent in fruit; tepals subequal, outer tepals slightly longer, 0.9–1.7 cm long, 2.0–4.0 mm wide; tepals whitish yellow centrally and dull green marginally on the inside, and dull yellowish white on the outside. Stamens nine, six in the outer cycle, three in the inner cycle, rarely totaling 10; filaments glabrous, dilated basally, divergent at anthesis, one-nerved, 4.2–5.2 mm long; anthers versatile, laterally dehiscent, 2.4–3.0 mm long. Gynoecium subdivided basally into three free stipitate carpels by an intercarpellary gland; lateral septal walls only appressed, unilocular along floral axis; styles short and free. Capsule erect, leathery, distinctly three-carpellate and dehiscence via septical separation; seeds numerous. Seeds reddish brown, glabrous, ellipsoidal with distal appendages; seeds 1.1–1.5 mm long, appendages 1.7–2.5 mm long. Flowering September to October; fruiting October to November. Locally abundant; pocosins, pine swamps and savannas of the southeastern coastal plain. Chromosome number unknown.

**Specimens Examined**

Florida: NW Florida, borders of swamps, September, A. H. Curtiss 15368 (MO); Near Argyle, bogs in pine barrens, 3 October 1901, A. H. Curtiss 6925 (MO).
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