STUDIES OF FLORAL MORPHOLOGY IN THE ERICALES—IV. OBSERVATIONS ON THREE MEMBERS OF THE GAULTHERIEAE

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The genera *Gaultheria, Pernettya, Chiogenes, Wittsteinia* and *Diplycosia* are frequently placed together as the tribe Gaultherieae, subfamily Arbutoideae, family Ericaceae. Occasionally they are included in the tribe Andromedeae of the same subfamily. *Gaultheria* contains approximately 100 species found primarily in eastern Asia and Central and South America; *Pernettya*, with 26 species, is found in the mountains from Mexico southwards (except for one species); *Chiogenes* (sometimes included in *Gaultheria*) has two species, one in northeastern North America, the other in Japan; *Wittsteinia*, with one species, and *Diplycosia*, with six, are found in the Malaya-East Indies region.

Chou (1952), in a paper dealing with various aspects of the floral morphology of three of the four species of *Gaultheria* found in the United States and Canada, reviewed the literature dealing with that genus, which thus need not be repeated here. The first paper of the present series (Palser, 1951) reviewed the literature on all the Ericales which had been published up to that time. Since then a few additional papers have appeared (Copeland, 1954; Creech, 1955; Palser, 1954). The present study deals with some aspects, particularly organography and vascular anatomy, of the flower of three additional species of the Gaultherieae: *Gaultheria hartwegiana* Klotzsch, *Pernettya mucronata* Gaud. and *Chiogenes hispidula* (L.) Torr. & Gray (the creeping snowberry of northeastern North America). The choice of these three species depended on availability at the time the work was started, not on any outstanding desirability of the particular species, except in the case of *Chiogenes*. As the eventual aim is familiarity with a large number of species for comparative purposes, each additional species studied becomes of interest in the total picture.

MATERIALS AND METHODS

The buds and flowers of *Gaultheria hartwegiana* were collected by Margery C. Carlson in Chiapas, Mexico. *Pernettya mucronata*, a native of Chile, was collected from cultivated plants in Corvallis, Oregon, at two different times by E. J. Kraus, and from cultivated plants in the Strybing Arboretum in San Francisco, California (with the permission of the superintendent, Mr. Eric Walther) on four different occasions by L. G. Kavaljian and by the author. *Chiogenes hispidula* was collected twice in northern Michigan bogs by the author and H. J. F. Gall, twice on Mt. Washington, New Hampshire (once by the author, and on a different occasion and in a different locality by S. K. Harris and the author), and in Harvard Forest, Petersham, Massachusetts, by W. H. Hatheway.

All specimens, except those in two collections of *Pernettya,* were killed and fixed in Navashin's solution, the two *Pernettya* in formalin- alcohol. All materials were infiltrated through an ethyl alcohol-tertiary butyl alcohol series and embedded in paraffin. Serial cross and longitudinal sections were cut at 10 μ and the majority stained with tannic acid-ferric chloride and safranin. A considerable number of buds, flowers and/or fruits of each species was sectioned: 29 of *Chiogenes,* 40 of *Gaultheria,* and 50 of *Pernettya.* All drawings were made using a camera lucida.

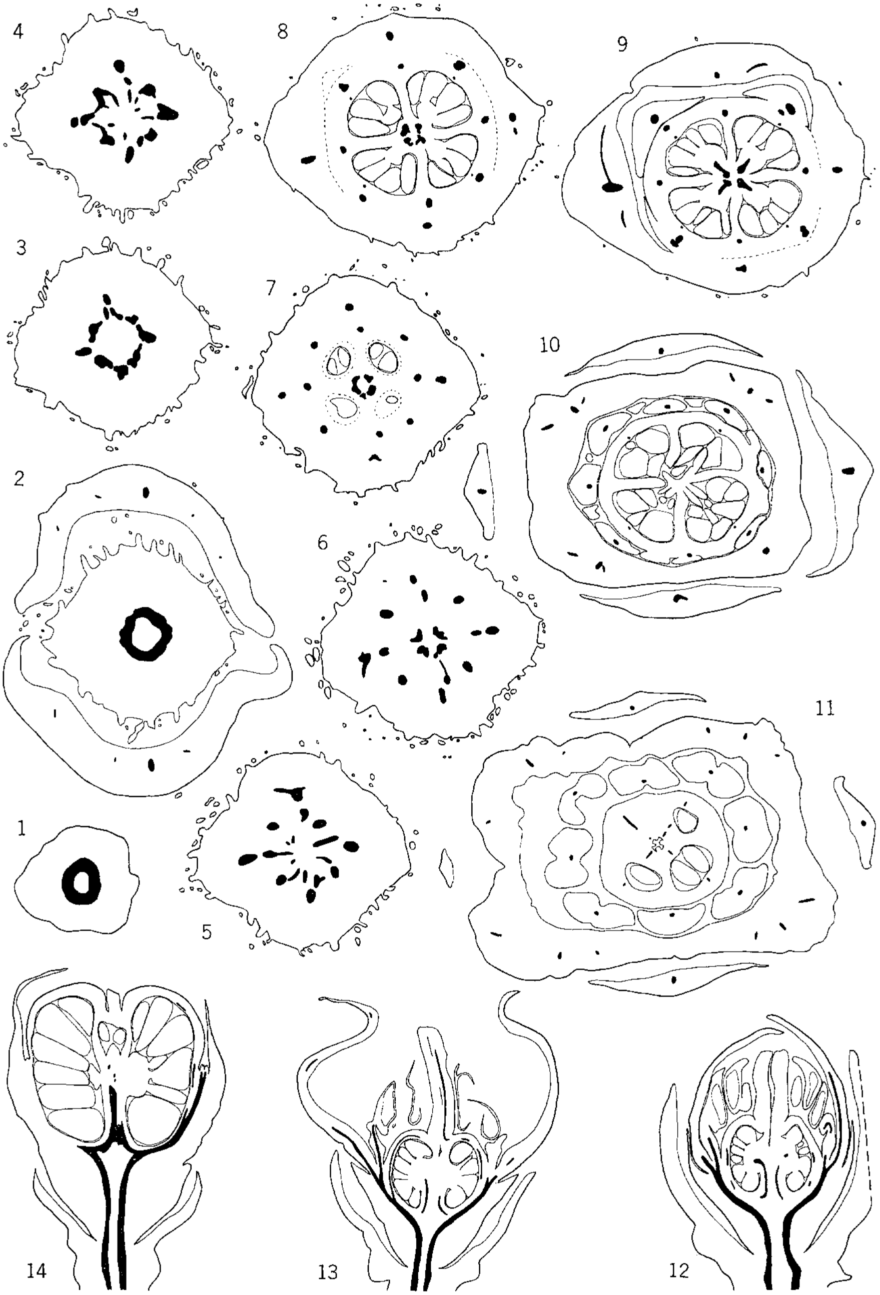
OBSERVATIONS

Organography.—A pair of bracts occurs on the pedicel immediately below the flower in *Chiogenes hispidula* (Figs. 2, 12-14), at a short distance below in *Gaultheria hartwegiana* (Figs. 15, 22) and at the base of the pedicel in *Pernettya mucronata* so that in the latter they do not appear in most sections. (In the following description the genus names alone will be used to refer to these species.) The flowers of *Gaultheria* (Figs. 15-23) and *Pernettya* (Figs. 24, 25) are pentamerous, pentacyclic (with the outer whorl of stamens opposite the petals), actinomorphic, sympetalous, urceolate and hypogynous. The five carpels of the compound pistil occur opposite the petals. *Chiogenes* (Figs. 1-14) differs in being tetramerous and half-epigynous. All three species have small nectariferous lobes on the ovary wall on either side of the sepalad stamens at the point where these become free (Figs. 10, 21). Placentation is axile in the species investigated but becomes parietal at the top of the ovary in *Gaultheria,* almost so in *Chiogenes,* but not in *Pernettya.* Carpel locules are continuous with the stylar canal. Ovules vary in number from 15 to 20 per carpel in *Chiogenes and Pernettya* and from 80 to 100 per carpel in *Gaultheria.*

All three show dermal appendages of some sort. In *Pernettya* a few unicellular hairs occur on the pedicel; in *Chiogenes* short, multicellular, multiseriate protuberances (Fig. 33) occur on the pedicel, bracts, and receptacle-ovary up to the point where the sepals become free; *Gaultheria* is extremely hairy, a condition which caused some difficulty in sectioning. Hairs of three sorts are found (Figs. 34-36): unicellular; long, uniseriate, multicellular; and very long, multiseriate, multicellular, and usually glandular. They occur primarily on pedicel, bracts, sepals, and petals (Figs. 15-23).

In *Pernettya* and *Gaultheria* the calyx is synsepalous for a short distance. When the sepals become free they show a slightly imbricate aestivation of the quincuncial type. *Chiogenes* also shows a slight synsepaly, but type of aestivation could not be determined. In all three the corolla has free limbs, longest in *Chiogenes* and shortest in *Gaultheria.* The aestivation of these in the bud is imbricate; two wholly in and two wholly out in *Chiogenes* and one wholly external, one wholly internal and three half and half in *Pernettya* and *Gaultheria.*

The anthers of all three species are introrse and extend upward beyond the four thecae in two short awns. In *Pernettya* each awn bi-



FIGS. 1-14.—*Chiogenes hispidula.* Figs. 1-11, diagrams of serial cross sections from pedicel to top of ovary, x63. In Figure 2 the pair of bracts, not included at higher levels, has been shown. Figs. 12-14, diagrams of longitudinal sections. Fig. 12, young bud, x67. Fig. 13, flower, x50. Fig. 14, fruit, x50.

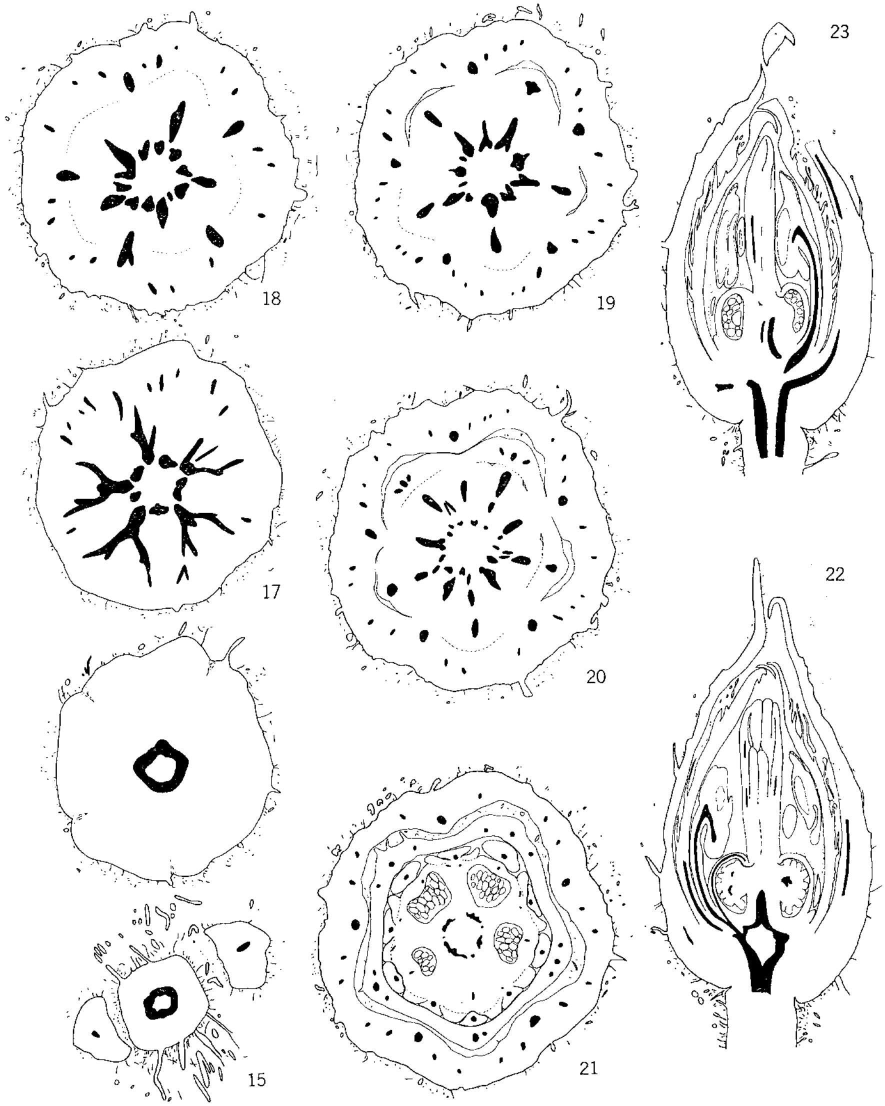
furcates close to the thecae, but this occurs only at the very tip in *Gaultheria* and *Chiogenes.* Each stamen in *Gaultheria* is characterized by a pair of pouches of highly granular cells which eventually disintegrate. These pouches are continuous from the lateral edges of the filament from a point just above the region of its attachment to the anther, through a protruding area of connective tissue, to a continuation of this connective tissue above the level of the thecae (*i.e.,* in the awns) where near the tip disintegration results in a bifurcation of each awn. Comparable granular pouches were not found in *Pernettya* or *Chiogenes,* but are reported and illustrated for other species of *Gaultheria* (Chou, 1952) and for some species of the Andromedeae (Palser, 1951). In all three, mature pollen grains are tetrahedral tetrads.

All three species are reported to produce "berries." A study of slides, as well as the literature, indicates that the nature of the fleshy tissue differs in each case. In *Gaultheria* the fruit is a capsule which is surrounded by a fleshy calyx; in *Pernettya* the ovary wall is fleshy and the calyx remains small; in *Chiogenes* the bulk of the fleshy tissue is derived from receptacle and joint carpel wall with other floral parts (Fig. 14) and in this respect is somewhat more comparable to the fruit of *Vaccinium* and its allies. Study of fresh mature fruits of *Chiogenes* should be made. If the free portion of the calyx becomes fleshy and the free portion of the ovary dry and dehiscent, a similarity to *Gaultheria* would be indicated; or if the calyx remains small and the free portion of the ovary becomes fleshy, there would be a similarity to *Pernettya.* There are some suggestions that the latter may be the case.

In studying a large number of flowers of *Pernettya mucronata* it became evident that either stamens or carpels were apparently not functional. In buds or flowers showing long stamens with functional anthers (Fig. 24) there were at most only one or two ovules per carpel and frequently there were none. On the other hand, in those flowers which showed several ovules, the stamens were short and the anthers collapsed with no signs of any sporogenous tissue (Fig. 25). The stigma is expanded in flowers with ovules (Fig. 25), not in flowers without (Fig. 24). All flowers or buds sectioned from any one collection were of the same sort, suggesting a functional dioecism such as has been reported for *Epigaea repens* (Palser, 1951; Stevens, 1911). Further studies should be made in the field and on herbarium material to determine whether this is consistent.

Vascular anatomy.—There are many similarities in floral vascular anatomy among these three species and between them and the various ericaceous flowers studied earlier. In all three the pedicel contains a complete ring of vascular tissue (Figs. 1, 15) which is interrupted at the point of departure of a single trace to each bract. The bract gaps soon close and a continuous ring is again found in the receptacle (Figs. 2, 16).

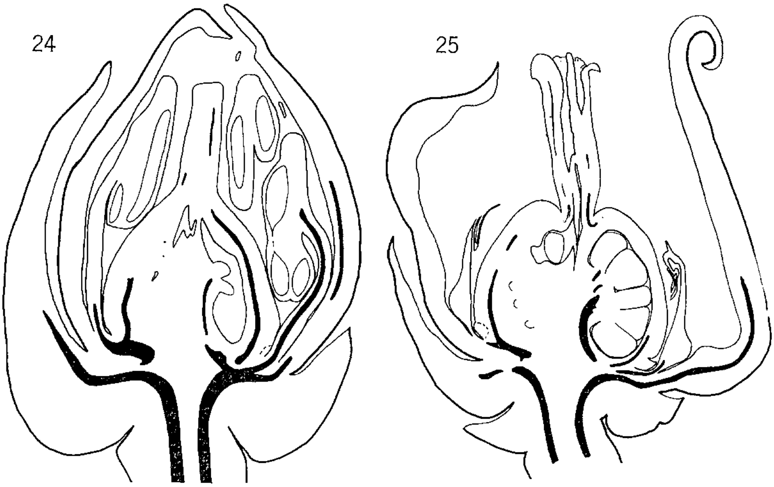
In *Pernettya* and *Gaultheria* vascular tissue to the sepals is the first to depart. Each sepal is supplied by a single large bundle, leaving a



FIGS. 15-23.—*Gaultheria hartwegiana*, x63. Figs. 15-19, diagrams of serial cross sections from pedicel to base of ovary. Figs. 22, 23, diagrams of longitudinal sections of same bud, several sections apart.

single gap in the vascular cylinder, which separates radially to three parts rather close to its point of origin (Figs. 17, 18). Additional branching of the laterals occurs. The lateral traces in particular turn downwards for a distance in their outward course. The size of the bundles and number of branches is greater in *Gaultheria* than in *Pernettya.* The petal traces form the next whorl of bundles, one trace to each petal (Figs. 8-10). Each gives rise to a total of three bundles at about the point where the corolla becomes free from the receptacle. The petalad stamen bundles are next to appear: in *Gaultheria* either as a single bundle after the closure of the petal gap or with a double origin, part from each side of the petal gap (Figs. 19, 20); and in *Pernettya* with the double origin, in some cases so close above the petal trace as almost to have a common origin with that bundle. Next the traces to the sepalad stamens arise, usually as single bundles after the closure of the sepal gaps. In each stamen of both whorls the single bundle traverses the filament and enters the connective where it turns downwards toward the apparent base of the anther (morphological apex, Matthews and Knox, 1926). Dorsal carpel bundles arise as single bundles from one side of the petalad stamen gap or essentially in common with the stamen trace in *Pernettya* and either as a single bundle from one side of the gap or as a double bundle from both sides of the gap in *Gaultheria* (Fig. 20). The dorsal carpel bundles pass upward through the ovary wall and into the style where they terminate just below the stigma. Vascular strands occur in the regions of the septa in *Pernettya* (Figs. 24, 25) arising close above or in common with the sepalad stamen traces. In the base of the ovary each of these strands gives rise to two or three bundles which traverse the carpel wall. Most of these terminate at the top of the ovary, but one or two frequently continue into and through the style. In *Gaultheria* a few very small bundles may arise from the sepalad stamen traces. These turn laterally and terminate near the nectary lobes (Fig. 21) and do not continue in the carpel walls. The remaining vascular tissue constitutes the ventral carpel traces, eventually forming five bundles in the mid-planes of the carpels. These enter the placentae and supply the ovules. It is interesting, and perhaps not too surprising, to note that in *Pernettya* all the carpel traces (particularly the ventral and septal) are more massive in those flowers which are functionally carpellate than in those functionally staminate.

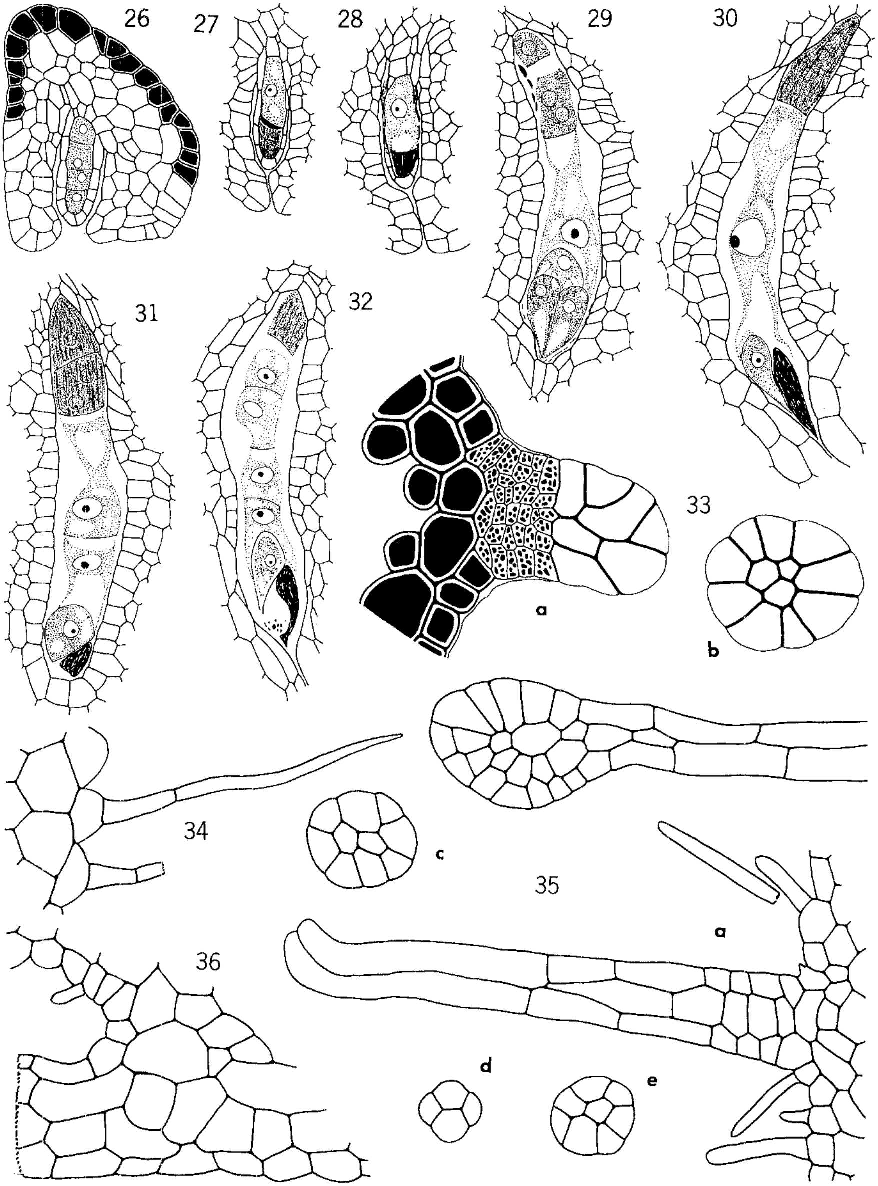
The vascular anatomy of the flower of *Chiogenes* differs in several respects from that described, the differences apparently ascribable, at least in part, to the fact that the ovary is half-inferior. The vascular pattern of *Chiogenes* is, in many ways, intermediate between that of *Gaultheria* and *Pernettya* described above and that of *Vaccinium* (paper in progress). Above the pair of bracts the receptacle broadens considerably, but the vascular traces do not diverge until just below the opening of the carpels (Figs. 2, 12-14). At that level four traces turn outward to supply the sepals (Figs. 3, 4). Occasional small laterals may



FIGS. 24, 25.—*Pernettya mucronata.* Fig. 24, diagram of longitudinal section of "staminate" bud, x63. Fig. 25, diagram of longitudinal section of "carpellate" flower, x43.

arise from these at various levels, but are not long. Slightly above and at what appears to be almost the same level, four bundles turn outwards between the sepal bundles and four other traces arise in the plane of the sepal bundles (Figs. 3-5). The latter supply the sepalad stamens and their origin is from one or both sides of the sepal gap; the former are compound bundles. At about this level small traces turn inward (Figs. 4-6), enter the ventral regions of the carpels and eventually the placentae (Fig. 9) where they supply the ovules. The compound bundles between the sepal and sepalad stamen bundles give rise inwardly to small strands, the dorsal carpel traces, above the level of the opening of the carpel locules. The remainder of each bundle separates tangentially to its two component parts, an outer petal and inner petalad stamen supply, only at the point where the floral organs become free from the carpel wall which is near midplacental level (Figs. 8, 9, 12-14). The petal traces divide to three up in the corolla a short distance (Fig. 10). The stamen bundles follow a course similar to that described for *Gaultheria* and *Pernettya.*

Ovule structure and development. —Material in all stages of development was not available for any of the three species studied. The ovules of the *Gaultheria* are small, unitegmic and anatropous. In *Pernettya* and *Chiogenes* they are larger, also unitegmic, and have a strong tendency towards the campylotropous condition. The only early developmental material available was in *Chiogenes* where a tetrad could be observed (Fig. 26), as well as stages in the disintegration of the micropylar spores and the enlargement of the chalazal one (Figs. 27, 28). Al-



FIGS. 26-33.—*Chiogenes hispidula*, x730. Fig 26, ovule with tetrad. Figs. 27, 28, disintegration of micropylar spores and enlargement of chalazal one. Fig. 29, mature megagametophyte. Figs. 30-32, endosperm development. Fig. 33, dermal appendage from bract: *a*, longitudinal section; *b*, cross section of tip. Figs. 34-36.—*Gaultheria hartwegiana*, x730. Fig. 34, uniseriate, multicellular hair on pedicel. Fig. 35, unicellular and multicellular, multiseriate, glandular hair from cross section of pedicel: *a*, longitudinal section of base only; *b*, longitudinal section of tip; *c*, cross section of tip; *d*, cross section in mid region; *e*, cross section near base. Fig. 36, base of multiseriate hair from longitudinal section of sepal.

though stages between these and the mature megagametophyte (Fig. 29) were missing, these are the critical stages and there is little doubt that the development can be classed as *Polygonum* type. The mature megagametophyte of *Chiogenes* (Fig. 29) is seven-celled and seven-nucleate, the secondary nucleus occurring close to the egg. The antipodals are quite large, the two micropylar nuclei sometimes separated by a wall and sometimes not. The occurrence of a single-layered nucellus in the tetrad stage (Fig. 26) would indicate that one archesporial cell had become a megaspore mother cell directly. The nucellus disintegrates along with the micropylar spores (Figs. 27, 28) and the megagametophyte comes to lie in direct contact with the integument (Fig. 29), as has been described for all other Ericaceae studied so far. The integument surrounding the chalazal half of the megagametophyte exhibits a weakly developed endothelium (Fig. 29).

The entrance of the pollen tube in *Chiogenes* destroys the synergids (Figs. 30-32). Division of the primary endosperm nucleus precedes that of the zygote, and endosperm development is cellular (Figs. 31, 32). The antipodal cells persist in a partially disintegrated state during the early stages of endosperm development (Figs. 30-32). Later stages show two endosperm haustoria, a micropylar and a chalazal one, both rather small. Developing seeds of *Pernettya* also exhibit both micropylar and chalazal endosperm haustoria, both larger than those in *Chiogenes* and separated from the body of the endosperm by very strong constrictions. The zygote in both elongates and develops into an embryo within the main body of the endosperm.

DISCUSSION

Particular interest attaches to *Chiogenes* which has had a long and varied nomenclatural history. (Airy-Shaw (1940) gave the following: *Vaccinium hispidulum* L., *Arbutus filiformis* Lam., *Arbutus thymifolia* Ait., *Oxycoccus hispidula* (L.) Pers., *Gaultheria hispidula* (L.) Muhlenb., *Gaultheria serpyllifolia* Pursh, *Chiogenes serpyllifolia* (Pursh) Salisb., *Glyciphylla hispidula* (L.) Raf., *Schollera hispidula* (L.) Steud., *Phalerocarpus serpyllifolium* (Pursh) G. Don, *Lasierpa hispidula* (L.) Torr., *Phalerocarpus hispidula* (L.) Heynh., *Chiogenes hispidula* (L.) Torr. & Gray.) While part of this history can be associated with determination of priority of both generic and specific epithets, much of it can be blamed on the real problem of the actual affinities of *Chiogenes* within the Ericales. As stated by Airy-Shaw (1940:328): ''The slight tendency of the ovary to become inferior is apparently responsible for the chequered nomenclatural career of this species''. Airy-Shaw felt that too much importance should not be attached to this character, as he found the same tendency in *Gaultheria semi-infera,* and thus he placed the plant in the genus *Gaultheria* in the series Hispidulae of the section Eugaultheria. The present author feels that the tendency is more than ''slight''; it occurs consistently in material collected from widely different localities and becomes more exaggerated as the flower becomes older (Figs. 12-14). "Half-inferior" flowers are also found in *Vaccinium;* the floral organs of the tetramerous *V. uliginosum* separate from the carpel wall at a point as low as, or only somewhat higher than, that in *Chiogenes.* This, however, is not an argument for placing *Chiogenes* with *Vaccinium.* The stamen characters are much more closely allied to the Gaultherieae than to the Vaccinioideae (or Vacciniaceae). In all members of *Vaccinium, Gaylussacia* and their allies so far studied in detail (44 species) the introrse anthers terminate upwards in a pair of very long awns which become hollow and partly open along one side near the tip and serve in the shedding of the pollen. In *Chiogenes,* on the other hand, the upward extensions of the anther do not become hollow or function as an opening for pollen dispersal. The separation of each awn into two parts at the extreme tip is accomplished by disintegration from the outside inwards and has no counterpart in the vacciniums. The author maintains *Chiogenes* as a separate genus (*C. hispidula* is the type species), allied to *Gaultheria* and *Pernettya,* because the differences between it and *Gaultheria* appear greater than those between *Gaultheria* and *Pernettya.*

The vascular anatomy of the flower in *Gaultheria hartwegiana* and *Pernettya mucronata* is more comparable to that of *G. ovatifolia* and *G. shallon* than to that of *G. procumbens* (Chou, 1952) in which there is essentially a single sepal trace. Both *G. hartwegiana* and the *Pernettya* show considerably less non-divergence of traces to the various organs than Chou (1952) reported for *G. procumbens, G. shallon,* and *G. ovatifolia* and thus might be considered more primitive. The extension of septal carpel traces into the style found in *Pernettya mucronata* also occurs in *G. ovatifolia.* This is not of common occurrence in the Ericales and has not been reported elsewhere in the Arbutoideae, although it is found in the Pyroleae and in *Sarcodes* (Copeland, 1941, 1947) and in *Clethra arborea* (Kavaljian, 1952). The large hairs of *G. hartwegiana* are similar to those of *G. shallon* (Chou, 1952).

Some differences in vascular anatomy between the species of *Gaultheria* and of *Pernettya* can be related to the portion of the flower which becomes fleshy in the fruit. Thus in *Gaultheria* the sepal traces are heavier and more subdivided, while in *Pernettya* the carpel traces are larger and more frequent.

What could be determined of ovule structure and development in *Chiogenes* was as expected. All previously studied material in the Ericaceae has shown anatropous to somewhat campylotropous, unitegmic ovules, a *Polygonum* type of megagametophyte development except in *Cassiope mertensiana* (Palser, 1952), an ephemeral nucellus, an endothelium, cellular development of the endosperm except in *Rhododendron japonicum* and *R. mucronatum* (Creech, 1955) and at least one, but frequently two, endosperm haustoria. Chou (1952) reported that large and persistent antipodals occur in the species of *Gaultheria* which she studied, comparable to those reported here for *Chiogenes.*

SUMMARY

1. Flowers of *Gaultheria hartwegiana* and *Pernettya mucronata* are pentamerous, pentacyclic, actinomorphic, sympetalous, and hypogynous. Anthers have short awns. Flowers of *Chiogenes hispidula* are tetramerous and half-epigynous.

2. Flowers of *Pernettya mucronata* are functionally imperfect and the plants may be dioecious.

3. The vascular anatomy of the flowers in the species of *Pernettya* and *Gaultheria* studied is quite similar, traces to the floral organs arising essentially independently in the following order: sepals, petals, petalad stamens, sepalad stamens, dorsal regions of the carpels (septal regions of the carpels in *Pernettya*), and ventral regions of the carpels. Each sepal trace immediately separates to three and the laterals again divide. Some septal carpel traces in *Pernettya* may enter the style; in *Gaultheria* small traces in a comparable position extend only to the base of the nectaries.

4. The vascular anatomy of *Chiogenes* differs from the above, apparently in association with its "half-inferior" condition, and appears intermediate between the above and the pattern found in *Vaccinium*.

5. What could be determined of ovule development agreed with observations made on other members of the Ericaceae: anatropous to somewhat campylotropous, unitegmic ovules, *Polygonum*-type megagametophyte development and cellular endosperm with haustoria.

6. For the present *Chiogenes* is maintained as a separate genus, the observable differences in the flower between it and *Gaultheria* being greater than between *Gaultheria* and *Pernettya*.

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