ONTOGENY AND COMPARATIVE ANATOMY OF THORNS OF HAWAIIAN LOBELIACEAE¹,²

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ABSTRACT

Carlquist, Sherwin. (Claremont Graduate School, Claremont, Calif.) Ontogeny and comparative anatomy of thorns of Hawaiian Lobeliaceae. Amer. Jour. Bot. 49(4): 413—419. Illus. 1962.—Species of Rollandia and Cyanea (sections genuinae and Palmaeformes), endemic Hawaiian genera of Lobeliaceae, are unique in the family in possessing thorns and thorn-like structures on leaves, and in some cases, on stems and flowers. These thorns always originate in conjunction with a unicellular, non-glandular trichome which terminates the thorn. Ontogenetic studies show that divisions leading to the formation of the thorn occur in the ground meristem as soon as the trichome is differentiated. Periclinal divisions predominate at first, but anticlinal and diagonal ones are also present at all stages. Thick secondary walls are formed on the trichome and other epidermal cells near the thorn tip. Periderm forms on old thorns of stems. Vascular tissue and laticifers are absent in thorns. Thorns in Cyanea and Rollandia seem best interpreted as specializations within these genera.

In Lobeliaceae, thorns on leaves, stems or flowers are present in only 2 genera, the Hawaiian endemics Cyanea and Rollandia (Wimmer, 1956). The writer studied thorns of these species as one phase of an anatomical investigation of Hawaiian Lobeliaceae, the anatomy of which has not been studied previously. In addition, a survey of literature on spines and thorns (e.g., Delbrouck, 1875; Schnee, 1939) reveals a remarkable lack of anatomical studies on thorns of various kinds. A number of papers deal with thorns or spines which are modified leaves, leaf-portions, or branch-tips. The thorns described in the present paper are distinctive in being, basically, unicellular trichomes raised on a conical mound of tissue derived from the ground meristem of stems, leaves, or flowers. Delbrouck (1875) described thorns which resemble those of Lobeliaceae in a number of Boraginaceae, such as Echium vulgare. He also shows that leaf teeth of Pandanus gramineus, Agave americana, and Lomatophyllum macrum possess a terminal trichome early in their ontogeny. The term “thorn” does not have a precise botanical usage. The term “spine” seems to be applied mostly to portions of leaves or to specialized leaves. “Thorn” as used in this paper has a topographical, not a morphological significance. The problem of defining thorns and thorn-like structures in Lobeliaceae is complicated by the fact that every intergrade between a relatively large thorn and a simple unicellular trichome may be found. Delbrouck (1875) admits all these intergrades as “Stacheln.” For purposes of simplicity, “thorn,” as used in Lobeliaceae, refers to a trichome raised upon a conical base formed from ground meristem.

Thorns of Lobeliaceae are limited to some species of Rollandia and species of 2 sections of the genus Cyanea. Several species of Rollandia have no thorns, although some (R. calycina) have small ones. Thorns are especially prominent in Rollandia St. Johnii, but they are comparable in size only to the smaller ones in the thorny species of Cyanea. Species of Cyanea which bear thorns belong to the sections Palmaeformes and Genuinae, as recognized by Hillebrand (1888), Rock (1919) and Wimmer (1956). The most prominent thorns occur in species of Genuinae such as C. ferox, C. Marksii, and C. nolimetangere, although in some of the Palmaeformes, such as C. aculeatiflora and C. hamatiflora, they are almost as conspicuous. In C. Marksii and C. nolimetangere thorns may be a centimeter or more in length. For a detailed survey of thorn distribution in Cyanea, see Rock (1919) or Wimmer (1956).

MATERIALS AND METHODS—Materials of Lobeliaceae were collected in the field and preserved in formalin-acetic-alcohol. Voucher specimens were also prepared. Specimens documenting the present study are as follows (herbarium abbreviations according to Lanjouw and Staffel, 1959): Cyanea aculeatiflora Rock, Carlquist 571 (RSA); C. atra Hillebr., Carlquist 569 (RSA); C. Marksii Rock, Carlquist 593 (RSA); C. trilomana A. Gray, Carlquist 601 (RSA); Rollandia calycina G. Don, Carlquist 575 (RSA); R. St. Johnii Hosaka, Carlquist H2 (UC). Additional species could have been studied, but sections of thorns in the above reveal the same basic structure and superficial observations on thorns in other species suggested no differences from this pattern.
CARLQUIST—THorns IN LOBELIACEae

Fig. 9–14. Thorn development in *Cyanea Marksii*: interpretive drawings of the sections shown in Fig. 1–6. Broken lines indicate probable recent divisions. Note that thorns form over strands of procambium. Dome-shaped formations in Fig. 9, 11, and 12 are mostly eminences associated with veins, whereas the projection in Fig. 14 is an actual young thorn base. All, ×370.

Material was sectioned by means of the usual paraffin techniques and stained with a safranin-fast green combination corresponding to Northen's modification of Foster's tannic acid–ferric chloride technique (Johansen, 1940).

ANATOMICAL DESCRIPTIONS—Ontogeny—*Cyanea Marksii* (Fig. 1–8; 9–14) was selected for illustrating ontogenetic studies because: (1) the numerous thorns, on both surfaces of leaves in this species, are more easily studied from sections of vegetative shoot apices than thorns on stems could be; and (2) this species has many stems, providing more shoot apices than the palmiform species. Sections of shoot apices of the palmiform species, *C. aculeatiflora* and *C. tritomantha*, showed the same features but provided fewer suitable stages for illustration. *Cyanea Marksii* is more densely covered with spines than other species; Fig. 8 shows the appearance of foliar thorns in this species.

As seen in Fig. 1, 9, formation of a foliar thorn begins with differentiation of a protodermal cell as a unicellular trichome. In species with large thorns, such as *C. Marksii*, divisions initiating the spine base occur simultaneously with the origin of the trichome. Although anticlinal divisions may be seen at any stage, periclinal ones predominate during early stages. Numerous periclinal divisions may be seen in Fig. 1–6, as interpreted in Fig. 9–14. As the mound of tissue underlying the trichome expands, cell divisions occur in various planes, increasing the volume of the thorn base.

Fig. 1–8. Thorn development in *Cyanea Marksii*—Fig. 1–6, Stages in expansion of trichome and underlying tissue. Fig. 1 shows early development of trichome. Shape of trichomes in Fig. 2–6 is probably altered by fixation, because mature stages (Fig. 7) are invariably conical, and some conical young trichomes may be found. Active cell division in subepidermal cell layers is occurring in the sections shown in Fig. 1–6 (see interpretive drawings and legend, Fig. 9–14).—Fig. 7. Trichome-tipped thorn on abaxial surface of young leaf, such as that shown in Fig. 8. Lamina below.—Fig. 8. Young leaf, seen from below. Note larger thorns on petiole; thorns are mostly restricted to petiole and zones along veins. All, ×600. Fig. 7, ×66. Fig. 8, ×4.
Early stages in thorn formation show divisions only underneath the trichome, but divisions extend to peripheral areas later. A wide thorn base is not built up at first. As seen in Fig. 7, a long, spindle-shaped thorn base forms. Widening of the thorn base takes place only during the last stages of thorn maturation, and is caused by cell enlargement. Divisions leading to thorn formation continue well past the stage at which procambium elements in the lamina have differentiated into protoxylem and protophloem (Fig. 6, 14).

The trichome which terminates a thorn elongates greatly during maturation, and develops a thick secondary wall, the outer surface of which is striate parallel to the long axis of the cell. Epidermal cells adjacent to the trichome base also develop secondary walls. This characteristic wall thickening accounts for the stoutness of thorns on the living plant. On herbarium specimens, epidermal cells with thick walls appear as a light-colored cap on the thorn.

Although thorns on leaves originate above and below future vascular bundles, their development is wholly the result of ground meristem divisions, and does not involve vascular tissue in any way. Study of large numbers of sections permitted this conclusion. Laticifers, which are abundant in the vegetative body of these Lobeliaceae, are absent in thorns. Significant in this regard is the fact that in Cyanea and Rollandia, laticifers are closely associated with phloem, so absence of vascular tissue in thorns might be expected to be accompanied by absence of laticifers. Breaking of the thorn on a living plant does not result in latex flow unless the entire thorn is broken off, thus damaging laticifer-bearing tissues beneath. Thus, thorns in Lobeliaceae are unlike the latex vessels of Cichorieae described by Zander (1896) and one may answer negatively Wimmer's (1956) query as to whether thorns of Lobeliaceae contain a "special sap."

Thorns on stems are longer-lived than those on leaves, and undergo further developments. Remnants of thorns may be seen on stems of old plants of palmiform Cyaneas such as C. macrostegia (Fig. 15-17). The stem of a young plant (Fig. 15) bears thorns which are anatomically the same as foliar thorns of C. Marksii. During aging of the stem, the terminal trichome of these thorns is lost (Fig. 17, right). Thick epidermal cell walls characterize old spines. Only a small increase in size, compared with thorns on a young stem, can be noticed. Eventually, the epidermis is broken in places, either by expansion of the spine or by injury by decay-causing microorganisms or by epiphytes. With damage of the epidermis, formation of a periderm occurs (Fig. 17). This periderm development is only moderately active, and although several layers of phellem may be developed, periderm action never produces notable corky excrescences. In very old thorns (Fig. 16), the periderm is partly lost, presumably by decay. At no time do thorns develop internal sclerenchyma. Firmness of the old thorns can be attributed only to succulence of the ground tissue parenchyma. In this respect, thorns of Lobeliaceae are quite unlike the thorns and spines of thorn-scrub and desert plants. Such thorns and spines are composed mostly of sclerenchyma (Schnee, 1939).

Comparative data—Studies were undertaken to determine what, if any, is the range in thorn anatomy among Hawaiian Lobeliaceae. The most obvious variation is one of size, for thorns may grade from relatively large structures such as those described above to trichomes only slightly raised upon an eminence. In all species examined, unicellular trichomes not accompanied by any evidence of thorn formation are present (viz, Fig. 21).

Unicellular, non-glandular trichomes have been reported in a number of Lobeliaceae (Metcalf and Chalk, 1950; Wimmer, 1956). Such trichomes were the only sort observed in Hawaiian Lobeliaceae of the present study. Close groupings of unicellular trichomes, which might be termed tufted hairs, were occasionally observed in Rollandia calycina.

Thorn-like structures may be present on the exterior surface of calyx and corolla, as in Cyanea aculeata (Fig. 18, 19). These "thorns" are often very soft and delicate, and are characteristic in long and narrow. Moreover, the unicellular trichome which terminates such thorns is thin-walled, as are the epidermal cells which surround it.

Structures which are not thorn-like, but are mound-like or knobby in shape occur on leaves and stems of Cyanea atra. Sections revealed that these structures (Fig. 20) appear to result from relatively late periderm action beneath unicellular thorns. Whether this periderm is a normal phenomenon or results from injury (e.g., fracture of the trichome) could not be determined. However, emergences of the nature of the one figured in Fig. 20 might be termed cork warts rather than thorns. True cork warts (Fig. 21) were observed in Hawaiian Lobeliaceae on the midrib of a leaf of Rollandia calycina. Periderm

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Fig. 15-19. Thorns of Cyanea spp.—Fig. 15—17. Cyanea macrostegia.—Fig. 15. Stem of young plant, showing prominent spines.—Fig. 16. Bark of old plant, showing degenerate thorns (light-colored spots).—Fig. 17. Median section of a thorn, from longisection of bark of an old stem. Terminal trichome base is still present, at right; periderm action evident below surface.—Fig. 18—19. Cyanea aculeata.—Fig. 18. Flower, showing spiny nature of calyx and corolla.—Fig. 19. Median section of smaller thorn from corolla lobe; from longisection of corolla. Fig. 15, X3; Fig. 16, X2; Fig. 17, X40; Fig. 18, X1; Fig. 19, X81.
Fig. 20–23.—Fig. 20. *Cyanea atra*. Transection of leaf, showing cork wart formation at base of trichome remnant (below).—Fig. 21–22. *Rolandiia calepina*.—Fig. 22. Cork wart from transection of leaf midrib. Uniseriate trichomes above.—Fig. 23. Transection of leaf, showing trichome on an emergence.—Fig. 23. *Rolandiia St. Johnii*. Near-median section of trichome on emergence, from leaf transection.—Fig. 25, X180; Fig. 21, X153; Fig. 22, X159; Fig. 23, X84.
formed as a response to injury by decay or attack by fungi or microorganisms was observed in various of the Lobeliaceae studied. Cork-wart formation as a result of injury to a trichome base would not be unexpected.

In the genus *Rollandia*, thorns are relatively small (Fig. 22, 23). Cell divisions which result in the formation of the eminences upon which trichomes are borne appear to occur relatively late in leaf ontogeny. As in thorns of *Cyanea*, epidermal cells surrounding the trichome develop thick walls. In *Rollandia calycina*, grouping of trichomes upon an emergence was occasionally observed. Only single trichomes were seen on thorns of *Rollandia St. Johnii*. Thorns are confined to the abaxial surfaces of leaves in *Rollandia St. Johnii*, and are present mostly on the abaxial surface, only sparingly on the adaxial surface, of leaves of *Rollandia calycina*.

**Significance of thorns**—The function which may be served by thorns of *Cyanea* and *Rollandia* is not readily apparent. Although insect predators are presumably present (especially in the form of larvae) in the Hawaiian rain forest, arguments could be advanced that these thorns would be relatively ineffective against depredation by these animals. Land snails (land snails) are indigenous to the Hawaiian Islands, and could conceivably be deterred by these thorns. However, the Hawaiian Islands are lacking in other herbivorous animals which would attack leaves and stems of Lobeliaceae. The fact that thorns of Lobeliaceae are succulent and lacking in latex suggests that thorns would be a better food source for predators than leaves or stems themselves, which contain large numbers of laticifers. Darwinian reasoning would suggest, however, that lobeliaceous thorns are not without function, for they have become highly developed in several species, and would be expected to have some selective advantage. Interestingly, seedlings of some species (e.g., *Cyanea tritmantha*) are provided with more and larger thorns than the adult plants.

From a phyletic standpoint, the distribution of spines in certain species of *Rollandia* and in some species of each of 2 sections of *Cyanea* is of interest. Thorns are absent in the remaining Hawaiian Lobeliaceae. Absence of thorns elsewhere in Lobeliaceae, and the specialized character of the species in which they occur suggest that presence of thorns is most logically interpreted as a specialization. From the anatomical standpoint, such an interpretation is supported by the fact that thorns represent derivatives, or elaborations, of trichome formations. The fact that thorns occur independently in *Rollandia* (which is probably closely related to *Cyanea*) and *Cyanea* suggests that this group of Hawaiian endemics has a tendency toward thorn formation which has been exploited in a remarkable way by some species groups, less prominently by others. This assumption is considerably easier to envision than a proposition that thorns were primitively present and have been lost in the majority of Hawaiian Lobeliaceae.

**LITERATURE CITED**


