ART. XIII.—*Chenopodium ambrosioides* L. *A morphological study;* by THEO. HOLM. (With 3 figures, drawn from nature by the author.)

According to Bentham and Hooker the small genus *Chenopodium* comprises not less than eight sections, among which *Blitum* L. The other sections, for instance *Chenopodiastrum* Moq., contain such species as *Ch. urbicum* L., *Ch. vulvaria* L., *Ch. polyspermum* L., *Ch. murale* L., *Ch. hybridum* L., and *Ch. album* L. In *Ambrina* Spach we have *Ch. ambrosioides* L., *Ch. multifidum* L., and a few others. The section *Botrydium* Spach was founded upon *Ch. botrys* L.; *Orthosporum* (R. Br.) upon some species from Australia; *Pseudoblitum* is *Blitum rubrum* Koch; *Rhagodioides* Benth. is Australian, and finally *Agathophyton* is B. *Bonus henricus* L.

These sections are based principally upon the floral structure; with exception of *Rhagodioides* "frutex spinescens," they are annual or perennial herbs, glabrous, farinose, or glandular pubescent; the members of *Ambrina* are "glandulosae, aromaticae." The number of stigmata is generally two, but from three to four in *Ambrina,* and from two to five in *Agathophyton.* The habit of the annual species is very uniform, but among the perennial, herbaceous the section Ambrina represents a type, quite interesting from a morphological point of view.

As a genus *Ambrina* was accepted by Torrey, but he included also *Ch. botrys,* and he considered *Ch. ambrosioides* specifically distinct from *Ch. anthelminticum;* by Gray, and also by Robinson and Fernald, *Chenopodium* is identical with the genus as proposed by Bentham and Hooker. And according to Gray's manuals *Ch. ambrosioides* is the species with *anthelminticum* as a variety.

Regarding the morphological structure of the shoot *Ch. ambrosioides* shows already from the seedling-state the structure, which is characteristic of the species. The seedling (fig. 1) shows a long, relatively thick, primary root with some very slender, sparingly branched, lateral roots; there is a short hypocotyl, and the cotyledons are epigeic, each with an axillary bud. The primary shoot

FIG. 1 TO FIG. 3.

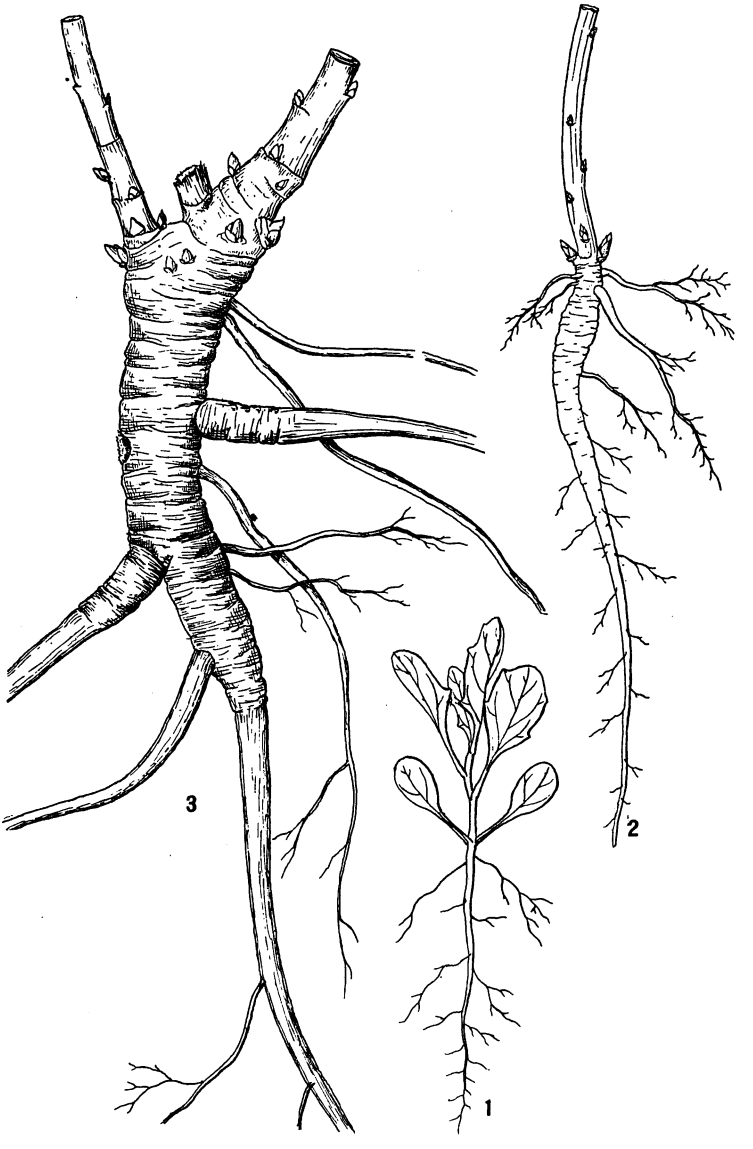

Fig. 1. *Chenopodium ambrosioides* L.; the seedling, about one month old; natural size.
Fig. 2. Same species; the seedling, about six months old; natural size.
Fig. 3. Same species; pseudo-rhizome of an old specimen, about four years old, showing the large, persisting, primary root with its strong lateral branches, and the stem-bases with buds; two-third of the natural size.

is erect, bearing several leaves. While the outline of the leaves of the mature plant is remotely sinuate-toothed those of the seedling vary from entire to sparingly denticulate. At the end of the first season, the latter part of October, (fig. 2) the seedling has developed into a tall, flower-bearing shoot, measuring a height of from 20 to 40 cm.; the root has also increased in length, c. 10 cm., and has become quite thick and wrinkled; it most frequently persists as a typical tap-root or with some few thick, lateral roots. At this state the plant is ready to winter over; while the aerial shoot dies down to near the base, the hypocotyl with the cotyledonary buds, and the root-system persists. The hypocotyl has increased somewhat in thickness, and has become pulled down into the ground by means of the contractile, primary root (fig. 2). In the succeeding spring the cotyledonary buds develop into flower-bearing shoots, and such may also be developed from the buds in the axils of the basal leaves of the primary shoot. When the plant is in its fourth year (fig. 3) we notice a large root-system, the primary measuring now c. 2 cm. in thickness, tapering gradually into a very long, thin root with some few strong, thick, lateral branches near the base. The hypocotyl is no longer distinct, but is represented by a thick, woody stem-portion with several persisting bases of floral shoots from the preceding year, and with numerous buds. In this way the plant consists now of several floral stems borne upon the same root, the primary of the seedling. In other words, we have in *Ch. ambrosioides* an excellent example of a "radix multiceps," or to use the classification proposed by Hjalmar Nilsson a "pseudo-rhizome," i. e. a complex of stem-bases. For according to this author the floral shoots develop here simply from buds in the axils of leaves borne upon the basal stem-portions, while in the rhizomes shoot, since it performs the function to store food-material for the development of this. While thus the aerial proper there is a subterranean stem, of which the structure is generally very distinct from that of the aerial shoots precede the development of the pseudo-rhizome, the sequence is exactly the opposite in plants with true rhizomes, since the development of the subterranean system of axes precedes the formation of the aerial shoots.

Chenopodium ambrosioides is thus a perennial plant in Virginia and Maryland, but it seems as if it occurs as an annual farther north. According to Torrey the species is said to be annual in New York, while the variety is described as a perennial; in the last edition of Gray's manual, the species is also said to be an annual, while the variety should be perennial at least southward. Regarding the occurrence of the species in Europe, it has been reported from several countries as an introduced, annual weed, for instance, in Germany according to Reichenbach (1830-1832), Doell (1843-1849), Koch (1857), and Wagner (1871); in Spain according to Amo y Mora (1871), and in central Russia (Lithuania) according to Ledebour. It has not, so far, been found in Denmark or Norway, but in Sweden, but only at a single locality near Halmstad according to Retzius (1774), "Crescit in plateis Halmstadi copiose, ut observavit Exper. D. Montin;" from this same locality we find it recorded by Liljeblad (1793), who states that the species is an annual; since then the plant has not been recorded, and was excluded by Fries in his Flora Scanica (1835). Nevertheless, it would appear as if *Ch. ambrosioides* had also been found near Lund in Skaane (the southern part of Sweden), for Linnaeus enumerates the plant in his Hortus Cliffortianus (1737) with the remark: "Crescit in Mexico. Perdurat hyemes Lundini in Scania ex hortis cum rejectaneis deleta; ubique circa urbem in stercorariis vulgaris facta et tota hyeme viret." None of the Swedish authors have referred to this statement by Linnaeus, which does not only constitute a new locality for this very rare plant in Sweden, but, furthermore, it does indicate, to some extent, that the species occurred as a perennial; the latter would be contrary to the diagnosis in Species plantarum (1753), according to which *Ch. ambrosioides* is annual, wherever it occurs. If the plant had really been found near Lund, we should expect to see it mentioned by Linnaeus in his "Skaanska Resa (1751)," for he visited Lund, and makes mention of some of the rare plants which he had found there 20 years earlier; but no reference is made to this particular plant. It is, therefore, undoubtedly correct, when Elias Fries (Flora Scanica 1835) expresses the opinion: "Vereor ne lapsu memoriae pro *Vulvaria* sit indicatum," with regard to the occurrence of *Ch. ambrosioides* near Lund.

If the species had ever existed there as a common weed, and even as a perennial, it could not possibly have escaped the attention of the numerous botanists who have explored that particular part of the country for so very many years. And owing to the fact, that Nordstedt in his recently published work, "Prima loca plantarum Suecicarum (1920)," credits Retzius for being the earliest author to mention the occurrence of the species within Sweden, there seems no doubt of the statement by Linnaeus depending on an error; but whether the locality given by Linnaeus was intended for some other plant, or whether "Lundini in Scania" was a misprint, we do not know.

The statements by the German authors, that it occurs only as an annual in Germany, are undoubtedly correct, for most of these authors were prominent morphologists, who barely could have overlooked the biological features of the species in question. The same may be the case on this continent, for Torrey was certainly an excellent observer, judging from the morphological treatment of the plants he described from the State of New York.

As a member of the flora of France, *Ch. ambrosioides* is enumerated and described by Lamarck and De Candolle (1805), but no statement is given with respect to it being an annual or perennial; at that time it was known from near Toulouse, Nantes and a few other stations; Grenier and Godron knew it only as an annual. Since then the species has been found at several other stations together with the variety *anthelminticum,* notably in southern France, and Alfred Reynier has contributed some very interesting papers, containing valuable information about the habit of these two plants. According to this author the opinion held by Gray that *anthelminticum* represents a mere variety of *Ch. ambrosioides* appears the most correct in view of the habit of these plants in France. Furthermore, this same author has observed that the species does occur as a perennial in France, and typically so. But it is very unfortunate that Mr. Reynier should take occasion to criticise Linnaeus for the statement in Hortus Cliffortianus, for as we have attempted to demonstrate in the preceding pages, it undoubtedly depends on an error.

So far as we know now, and with certainty, *Chenopod-*

ium ambrosioides is typically a perennial plant on this continent (Maryland and Virginia) and in France. Farther north it becomes an annual on both continents. Such is the case, however, of numerous other plants. We need only to cite Lamarck and De Candolle (l. c. Principes de Botanique, p. 222) "Des plantes bisannuelles deviennent annuelles dans les climats chaudes; des plantes vivaces, telles que le ricin et la belle de nuit, deviennent annuelles dans les climats froids." A very comprehensive paper dealing with this subject, the vitality of certain plants, has been contributed by Friedr. Hildebrand. According to this author many species of *Cruciferæ, Compositæ* and cultivated *Gramineæ* show a tendency to vary from annual to biennial, besides that some typically biennial species may occur as perennials, notably among *Cruciferæ, Umbelliferæ, Papilionaceæ cet.* While *Cyperus flavescens* has been described as an exclusively annual plant in Europe and this continent, it occurs also as a perennial in Maryland and Virginia, beside that Lange found some stoloniferous specimens of the species in France; as shown by Irmisch *Hyoscyamus niger,* while typically biennial, may occasionally occur as an annual, and this annual form has been described as a proper species: *H agrestis,* since the habit is very different.

Internal Structure of the Vegetative Organs.

The very peculiar structure that characterizes the root and stem of a number of *Chenopodiaceae* was noticed already by Unger (1840) and since then several other authors have made a special study of these plants; we might cite, for instance, Gernet, Regnault, Naegeli and Leitgeb, Duval Jouve, Van Tieghem, Georghieff, and finally, Fron; a general sketch of the anatomy is given by Solereder in his comprehensive work on the anatomy of the Dicotyledones.

The Root-System.—The capillary, lateral roots of the seedling, as well as of the mature specimens, are of short duration, and do not increase in thickness. Their structure is perfectly normal: the epidermis is hairy, the narrow zone of cortical parenchyma (one to two strata) is thinwalled; the endodermis and the pericambium show the usual, thinwalled structure, and the stele in diarchic.

A similar structure recurs in the very slender apex of the primary root of the seedling before secondary tissues become developed. While thus the structure is normal from the beginning, the increase in thickness is effected in such manner, that the arrangement and development of the tissues, and the mestome-strands especially, become quite anomalous. This may be seen, if we examine the basal portion of the primary root of the seedling. We notice then, that the epidermis, the cortex, and partly also the endodermis have become thrown off, and replaced by a large, meristematic tissue, extending to the stele; a circular band of very thin leptome-strands is located in this tissue, which owes its origin to the pericambium. As we remember from roots with normal structure the function of the pericambium is to develop lateral roots, the secondary cortex and the cork; but in *Chenopodium* there is inside the secondary cortex a meristematic tissue, which gives rise to concentric bands of mestome-strands. In no parts of the primary root of the young seedling (fig. 1) does the increase extend beyond the development of the meristem and the first band of mestome-strands; the cork is either not developed or present as a single stratum.

A still more advanced structure is to be seen in the thick primary root of the older seedling (fig. 2), which is about to winter over. There is now a broad, peripheral zone of homogeneous, thinwalled cork, surrounding a large, thinwalled parenchyma filled with starch. The primordial stele is still preserved, but around this are now two concentric bands of collateral mestome-strands, developed from the meristem, and separated from each other by bands of parenchyma. By continued growth of the root the peripheral portion of the meristematic tissue gives rise to a new band of mestome-strands, thus the final structure of the thick roots of mature specimens shows several concentric bands of mestome-strands and thinwalled parenchyma containing starch and crystalline sand, very fine as well as coarse grains. Regarding the structure of the mestome-strands the vessels form linear rays (in transverse sections) with a large strand of thinwalled libriform on the inner face. The old stele persists and contains much thickwalled libriform around the vessels.

Chenopodium ambrosioides thus represents the type of root-structure, where the increase is effected by successive circles of meristematic tissue. It is a structure common to many species of the Chenopodiaceae, and has been described so admirably by Van Tieghem in Beta. In some of the other genera (*Salicornia* and *Obione*) the meristem represents only short arches as described by Fron. And considering the root-structure altogether in this family Fron has shown that while the structure is most frequently symmetric, an asymmetric is characteristic of several species.

The Stem.—At the seedling-state the structure of the young internodes is perfectly normal. In the apical internode a smooth cuticle covers the epidermis of which the outer cell-wall is slightly thickened; glandular hairs abound; they are very short consisting of a pluricellular (in one row) stalk and a large, ovid, unicellular head. The stem is somewhat angular with hypodermal collenchyma in the ridges; otherwise the cortex is thinwalled, and some of the cells contain fine, crystalline sand. There is a very distinct, thinwalled endodermis, destitute of starch, but here and there with crystalline sand. A pericycle is also distinct, and consists of several strata, partly parenchymatic, and partly stereomatic. The stele contains about ten collateral mestome-strands, separated from each other by broad rays of parenchyma. A homogeneous, thinwalled pith with starch and crystalline sand occupies the center of the stele.

The first indication of the anomalous structure appears in the internode below the apical, where the peripheral layer of the pericycle has begun to divide itself tangentially, giving rise to a thinwalled meristem. Otherwise the structure of the other tissues agrees with that of the apical internode.

Further down the stem of the same seedling, for instance in the epicotyl, we observe a wrinkled cuticle, a weaker structure of the collenchyma, and the first appearance of cork, which arises from the hypodermal stratum of the cortex; starch and crystalline sand occur in the cortex. Regarding the pericycle this has now developed many layers of parenchyma in radial rows, in the peripheral portion of which small strands of leptome have become differentiated, but, so far, no hadrome. The internode above the epicotyl lacks cork but pos-

sesses more collenchyma. It deserves notice, that an endodermis was observed in all the internodes of the seedling.

While the apical internodes of the thin, flower-bearing branches of mature specimens show the same structure as the apical of the seedling, and with a distinct endodermis, this sheath is not developed in the thicker portions of the stem. In the thick internodes of mature specimens several modifications are to be observed. The collenchyma is well represented in the ridges; the cortex is heterogeneous, consisting of three peripheral, chlorophyll-bearing strata covering a few strata of much larger cells, but destitute of chlorophyll. There is no endodermis, and the pericycle has now given rise to a circular band of small mestome-strands outside the primordial; cells with crystalline sand were observed in both cortex and pith. A similar structure recurs in the very thick internodes of old specimens, but in these we find an incomplete sheath of stereids (a single layer) between the colorless cortex and the meristem. The stele shows here three confluent bands of mestome-strands outside the primordial, and developed in the same manner as in the root. Finally may be mentioned that cells with fine as well as coarse, crystalline sand occur in the parenchyma, and in longitudinal sections these cells were seen to be placed on top of each other, in rows of considerable length.

The Leaf.—Glandular hairs of the same structure as those of the stem abound on both faces of the leaf-blade. Stomata, level with the epidermis, occur on both faces, most frequently, however, on the dorsal; the cuticle is wrinkled above the midrib, but otherwise smooth and thin. Viewed "en face" the lateral cellwalls of the epidermis are strongly undulate on the dorsal face, much less on the ventral. The epidermis is thinwalled, except in the midrib, and the lumen of the cells slightly wider on the ventral face. A single stratum of short, somewhat irregular, palisade-cells cover three layers of pneumatic tissue interspersed with cells containing crystalline sand. The midrib contains a little collenchyma on both faces, and a large water-storage-tissue completely enclosing an arch of mestome, and of stereome on the leptome-side. The petiole is in cross-section quadrangular with two

narrow wings, but the structure agrees with that of the midrib, except that the mestome is represented by five separate strands.

Concerning the anatomical structure of the genus *Chenopodium* we have learned from the work of Fron that the symmetrical structure of the root is characteristic of some species, the asymmetrical of others. And with respect to the stem and the leaf, as pointed out by Solereder, the hairs show several interesting forms, among which the secreting, glandular are especially characteristic of the sections: *Ambrina* and *Botrydium*. While none of the genera possess internal, secretory ducts, we find calcium oxalate as aggregated crystals or as crystalline sand in several species of the family. The anomalous structure recurs in the stem of the species, which shows a well-marked increase in thickness, and reminds of that of *Nyctagineæ* and *Amarantaceæ*. Several authors have treated the extreme types of the family, especially those of the deserts and sea-shores, and many highly interesting structures have been described. But with regard to the less conspicuous, the annual weeds, these have, so far, attracted but little attention from an anatomical point of view.

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