Contents

Introduction

This work is the culmination of a lifelong fascination with these remarkable plants. As a boy growing up in the farming area just north of Detroit, I was first attracted to their unique seedpods and their copious milky sap. I had read that the sap could be dried to become a chewing gum like chicle; and that the down from the seeds had been used to stuff life jackets during WWII. I had wanted to try these out for myself, but nothing ever came of it. I don't recall paying much attention to their equally-unique flowers. When I went to Michigan State University, I took John Beaman's introductory course in plant taxonomy and became more aware of the differences between flowers and how they could be used to indicate relationships between plants. Still, I don't recall seeing any species at that time other than *A. syriaca* and *A. incarnata*, though there should have been several others in the area.

At the University of Maryland I did encounter two other species: *A. viridiflora* and *A. tuberosa*, and my interest expanded. I also began studying the flowers and drawing them. At the University of Florida I soon discovered a new wealth of species; *A. cinerea, A. pedicellata, A. curtissii, A. lanceolata, A. longifolia, A. tomentosa, A. humistrata, A. perennis* and other genera as well; *Cynanchum, Sarcostemma, Ceropegia, Hoya, Matelea.* I xeroxed **Woodson's** entire 1954 monograph, bound it together, and bought myself a Nikkormat camera with a macro lens. Soon I was photographing them all over the state.

After graduation I joined the Peace Corps and went to teach botany at the agricultural college near Kuala Lumpur. I soon found that Malaysia was a paradise of Asclepiadaceae. The largest genera were *Hoya* and *Dischidia,* but there were many others as well; *Tylophora, Gymnema, Sarcolobus, Atherandra, Ischnostemma, Dregea, Finlaysonia, Gymnanthera, Streptocaulon, Secamone, Genianthus, Lygisma, Toxocarpus, Heterostemma, Pentasacme, Gongronema, Ceropegia,* even *Calotropis gigantea* and *Asclepias curassavica.* I monographed the local species of *Hoya* for the *Malayan Nature Journal* and those of *Dischidia* for *Blumea.*

When I returned I went to work for Everglades National Park, but it was such a letdown after Malaysia that I didn't stay there long. I then went to work for the Rijksherbarium at Leiden, The Netherlands, and monographed the genus *Sarcolobus* for *Blumea.* It was strictly a herbarium study of plants I'd never seen alive and I found that I greatly missed the field work. In spite of their reputation for liberality, I found the Dutch remarkably intolerant people and our parting was mutual. While there, though, I did get to converse with Max van Balgooy, Marius Jacobs, Roloef van Urk, Ruth van Crevel, Ding Hou (Woodson's assistant on the *Asclepias* monograph) and others whose names I have forgot-

ten, but whose kindness I have not. In England I met R. E. Holttum, John Dransfield and David Fields, and have fond memories of them.

Back in the US, I went on to other things until my father died and left me an inheritance. I realized that if I managed it well I now had the oportunity to work on any project of my choosing. Looking through my old copy of Woodson, I saw that I was actually unfamiliar with most of the North American species of *Asclepias*, and that his monograph, written solely for other scientists and buried in the *Annals of the Missouri Botanical Garden*, was essentially unavailable to the many serious milkweed enthusiasts among the general public. I have long held the view that publicly-funded science should be more accessible to the serious amateur. So, I decided to do a more user-friendly update of Woodson's monograph, with a history and illustrations of each species. To accomplish this, I needed to translate articles in Latin, German & French, so I taught myself to read those languages. I have spent many hours in herbaria and I recognize their value to science. But I also recognize their limitations; the plants in them are dead, crushed flat, plant mummies and, in such a state, can be easily misinterpreted. I am a naturalist and I wanted to do a study of living plants. To this end, I travelled across the US and located members of each species, saw where and how they were growing, photographed them, collected & dissected flowers from each species. In doing so, I travelled well over 100,000 miles over a 10 year period. I loved being out in remote places searching for these remarkable plants & learning all I could about them. And that fascination is what I have tried to present here. Some of the species were difficult to find and I sought & received help from many people. True, there were some who, when queried, considered me an intruder into their elite world, and refused. However, thanks to the internet, it was fairly easy to circumvent these people. I express my gratitude to the following people, all of whom helped this project in some way, even if only by having an herbarium sheet with an accurate location on it in one of the herbaria I visited.

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I am, of course, most indebted to **Robert Everard Woodson Jr.** and his assistant, **Ding Hou**, for his splendid paper; his careful searching out of the synonomy, and his range maps, which I have expanded and updated, were an enormous assistance.

Here are three quotes that express how I feel about this study:

The lepidopterist, **Vladimir Nabokov**, in a letter to Elena Sikorski 11-26-45, noted that "My work enraptures but utterly exhausts me; I have ruined my eyesight, and wear horn-rimmed glasses. To know that no one before you has seen an organ you are examining, to trace relationships that have occurred to *no one* before, to immerse yourself in the wondrous crystalline world of the microscope, where silence reigns, circumscribed by its own horizon, a blindingly white arena—all this is so enticing that I cannot describe it."

Thomas Henry Huxley, Darwin's bulldog, was quoted as saying,

"I am not interested in seeing what no one has ever seen before, but rather in thinking what no one has ever thought before about what everyone has seen."

In 1836 **Washington Irving** published ASTORIA and in Chaper 17 noted that "Mr. [Thomas] Nuttall seems to have been exclusively devoted to his scientific pursuits. He was a zealous botanist, and all his enthusiasm was awakened at beholding a new world, as it were, opening upon him in the boundless prairies, clad in the vernal and variegated robe of unknown flowers. Whenever the boats landed at meal times, or for any temporary purpose, he would spring on shore, and set out on a hunt for new specimens. Every plant or flower of a rare or unknown species was eagerly seized as a prize. Delighted with the treasures spreading themselves out before him, he went groping and stumbling along among a wilderness of sweets, forgetful of everything but his pursuit, and had often to be sought after when the boats were about to resume their course. At such times he would be found far off in the prairies, or up the course of some petty stream, laden with plants of all kinds.

The Canadian voyageurs, who are a class of people that know nothing out of their immediate line, and with constitutional levity make a jest of anything they cannot understand, were extremely puzzled by this passion for collecting what they considered mere useless weeds. When they saw the worthy botanist coming

back heavy laden with his specimens, and treasuring them up as carefully as a miser would his hoard, they used to make merry among themselves at his expense, regarding him as some whimsical kind of madman."

I also learned that when someone says "It's all over the place," they really mean "I may have seen one there once." And when they say "You can't miss it," they really mean "I never could find it again, but maybe you'll be lucky." I ran down many false leads.

History

The generic name of *Asclepias* is an almost exact rendering of the Greek word **Ἀσκλήπιος**. It was first mentioned in the ILIAD of **Homer** [800 BCE] where it may have referred to an actual person. In Greek mythology Asklepios was the son of Apollo and Coronis. He became such an adept physician and saved so many lives that Pluto feared he would render men immortal. Hence, at his urging, Zeus killed him with a bolt of lightning. He was symbolized by a staff entwined with a snake and grateful devotees customarily sacrificed a cock in his honor. His daughter, Hygieia, was the goddess of health. The last recorded words of **Socrates** [399 BCE] were: "Crito, I owe a cock to Asklepios. Will you pay the debt for me?" In 116 CE the Roman historian **Tacitus** [ANNALS 12.61] noted that "by the arrival of Æsculapius, the art of the physician was introduced, and was practiced with much fame by his descendants [on the island of Cos].", He was a favorite diety of the Roman emperor **Diocletian** [300 CE].

Somewhere during this time, the name also became attached to a highly-regarded medicinal plant and was included by the Greek physician, **Pedanios Dioscorides** [50 CE], in his work DE MATERIA MEDICA. It was considered of great effectiveness for poisonous bites & stings and acquired the Latin name of *Vincetoxicum* [literally, it conquers poison]. Its typical milkweed seedpods with their downy seeds reminded some folks of swallows, and it also came to be known as Swallow-wort. Sometime in there, too, the final vowel became an "a". All of the medieval herbals included it, some with excellent illustrations. During this time all plants with such seedpods were either considered a form of *Asclepias* or of *Apocynum*, with the 2 names used interchangeably. When **Gerard** described the first North American milkweed in 1597 he called it the *Indian Swallow-wort* or *Asclepias virginiana* or *Vincetoxicum Indianum*. But when **Cornut** described the second one in 1635, he called it *Apocynum majus syriacum rectum*. This confusion was not cleared up until 1753 when **Linnaeus** put

the plants with bell-shaped flowers into *Apocynum* and those with star-shaped flowers into *Asclepias*. The European milkweed became *Asclepias vincetoxicum* and **Cornut's** American milkweed became *Asclepias syriaca*.

Linnaeus had placed 18 species into *Asclepias*, but as more species were added to it, it became a collection of disparate elements. By 1798 **Karl Willdenow** compiled the genus with 41 members, some of them from Africa and India. In 1794 the German botanist, **Conrad Moench,** removed the European milkweed from *Asclepias*, where it did not belong, and made it *Vincetoxicum officinale*. But in 1805 the South African mycologist,**Christiaan Hendrik Persoon,** made it *Cynanchum vincetoxicum*. Both names are currently in use; GRAY'S MANUAL OF BOTANY (1950) uses the **Persoon** name; FLORA VON DEUTSCHLAND (1885 & 1905) the **Moench** name.

During the 19th century as more new species were described, the genus *Asclepias* was refined and purged of its most obviously disparate elements (*Calotropis & Hoya* in 1811). In 1952 the English botanist, **Arthur Allman Bullock,** removed the African species and it became an American genus. But the trend of splitting off genera continued with some of the American members taken out and placed in other new genera. By 1940 there were 20 genera allied with *Asclepias*, most of them with only 1 or a few species. For example; originally described as *A. viridis* by **Walter**, it was placed in *Podostigma* by **Elliott** and in *Asclepiodora* by **Gray**; originally described as *A. viridiflora* by **Rafinesque**, it was placed in *Acerates* by **Elliott**, while other authors had it in *Gomphocarpus, Polyotus & Otanema*. To most observers, the differences between *A. syriaca* and *A. viridis* are certainly large enough to merit separate genera, but, as **Woodson** pointed out in his 1941 paper entitled THE NORTH AMERICAN ASCLEPIADACEAE in vol. 28 of *Annals of the Missouri Botanical Garden* "a narrow concept of coronal structure as a criterion of genera, if persued consistently, will lead to a multitude of monotypic entities...that few genera will consist of more than 2 or3 species, and that each new species will introduce anew the question of generic differentiation."

In 1885 the German botanist & botanical artist, **Otto Wilhelm Thome**, published a lavishly illustrated FLORA VON DEUTSCHLAND, ÖSTERREICH UND DER SCHWEIZ which included this superb illustration of the original *Asclepias*.

487 *Vincetoxicum officinale Monch* Gemeine Schwalbenwurz.

And so, in 1954 **Robert Everard Woodson, Jr.,** a botanist at the Missouri Botanical Garden in St. Louis, completely redefined the genus in his monumental paper THE NORTH AMERICAN SPECIES OF ASCLEPIAS, published in the *Annals of the Missouri Botanical Garden*, Vol. 41. **Woodson** elliminated the other 20 genera; in doing so, he had to broaden the definition of the genus to encompass these variations. I have reworked and expanded his definition as follows:

ASCLEPIAS. Perennial herbs, germinating epigeally, rarely hypogeally, rarely annual or woody, usually lactiferous. Roots thick-fibrous, fleshy, or gemmiferous-spreading. Stems erect or decumbent, solitary or clustered, glabrous or pubescent. Leaves decussate or rarely in one plane, sometimes whorled, or irregularly approximate; margins entire, often undulate, chartaceous to coriaceous, sessile or petiolate, apex acute to obtuse or emarginate, base acute to cordate; glabrous to villous. Umbels terminal and solitary, to many, erect or nodding; or lateral, 1—many; sessile or pedunculate. Flowers 1—few, or many; pedicellate. Calyx of 5 equal lobes, divided nearly to the receptacle; bearing few to many tiny glandular squamulae within at the base. Corolla rotate, of 5 lobes, valvate or imbricate, reflexed, spreading, or rarely erect. Gynostegium subsessile to stipitate; corona of 5 hoods attached to the column and subtending the connivent anthers; the hoods cucculate to clavate with various modifications, stipitate to sessile and deeply saccate at the basal attachment to the column, or solid; usually bearing an internal horn or crest; anthers 2-locular, with more or less prominent corneous marginal wings enclosing the 5 stigmatic chambers & with membranous apical appendages, subtended at the base by a variously-shaped nectar cover; the pollinia paired & pendulous from the often geniculate translator arms, flat & uniformly fertile, enclosing granular pollen; stigma head truncate, peltate, pentagonal. Fruit a follicle, erect on erect pedicels, erect on deflexed pedicels, or pendant; seeds many, compressed, comose or rarely naked, imbricate within the follicle.

This description contains a great many "ors" due to the great diversity of forms that it includes. But there are unifying features that unite nearly all members of the genus. 1) All have leaves with entire margins. 2) All have an appendage attached to the filament column of the anthers, called a hood. 3) In all but three, the hoods contain either a horn or a remnant of one in the form of a crest or a median lobe. 4) The apex of the stigma is truncate or slightly concave. 5) Each pair of anther wings is subtended by a nectar cover. 6) The pollinia are flat, and many of the translator arms are geniculate just above their attachment to the pollinia.

Taxonomy

Science is an ongoing process; it has a beginning, but will not end until civilization here does. In plant taxonomy we can usually tell when and by whom a plant was named; but it is not always so simple to decide which name is the correct one for a given plant, because it may have been named several times by several different people. It may have been collected in Virginia by an Englishman, described in English, and the specimen deposited somewhere in England or Scotland. The same species may also have been collected in New York by a Frenchman, described in Latin or French, and the specimen deposited somewhere in France. Or it may also have been collected in Pennsylvania by a German, described in a German journal, and the specimen sent to a patron in The Netherlands. It is a tedious process to search out all of these specimens, translate the descriptions, and decide which one should be the valid name. The specimen may be lost; it may have no flowers; it may be undated; it may be damaged and indeterminable. People also make mistakes. The strangest one that I encountered was by the English botanist, **Henry Nicholas "Rubber" Ridley,** in his FLORA OF THE MALAY PENINSULA. He described a species, *Hoya occlusa*, with unopen buds, saying, " the buds seem never to open." This would be absurd for a *Hoya*. When I found the specimen at the Singapore Herbarium, I moistened a bud and opened it; it was *Hoya coriacea*. It happens all the time, to all of us. You need only recall the "cosmological constant" of **Albert Einstein**. I will point out errors that I have found while doing this study. In the process, I will also have made some of my own; I urge you to be on the lookout for them. In my discussion of each species, I have presented its taxonomic history in some detail to show how this happens and why there are sometimes different names for the same species. I know this can seem confusing and annoying, since we crave certainty, but this is the way it is, so get used to it. Now that plant taxonomy is moving on to the molecular level with rna analysis, this may change, but it will take a long time to see it.

Classical plant taxonomy is an inexact science; it requires value judgements as to the relative importance of the various characters. Hopefully, the botanist will choose his characters carefully and select the least variable ones to base his relationships on; but it is common to see botanists attaching importance to such highly variable characters as vestiture, leaf shape & size, flower color & size, while ignoring other more conservative characters as pollinaria, flower structure, habit and habitat. On page 9 **Woodson** noted that "The most variable structure of asclepiadaceous flowers is the corona..." On page 24, "considerable variation is found, and one must not consider the flower drawings accompanying this revision as inviolable patterns from which all individuals of a species are cast." Yet he then goes on to make this most variable structure the basis of his taxonomic scheme, and maintains it even when it gets him into difficulties. He didn't seem able to entirely free himself from the past. This is odd because he

had so many other original observations. For example, on page 17 he noted that there are "special notches or spurs indenting the [anther] wings and characteristic of certain species." Yet he ignored them taxonomically, and treated them only as a curiosity when he encountered them.

Another problem is the use of pressed, dried specimens to determine the relationships between living plants. On these sheets the plants and especially the flowers often appear different than they do when fresh and alive and some characters can be difficult, even impossible, to accurately determine from them. Many errors have resulted from this and so I have photographed each species in this study in its natural habitat and dissected flowers that I collected and preserved in FAA.

Woodson did not quote **Edward Lee Greene** in his monograph though he must have read his views ON THE CLASSIFICATION OF ASCLEPIADS. It was published in 1897 in Vol. 3 of *Pittonia*, and I include it here.

"That notable multiplication of genera which marks the recent history of the Asclepiadaceae has proceeded as it were in violation of one of the most firmly established principles of taxonomy; the principle that plants are related in the ratio of the similarity of their fruit-structure; that plants whose fruits are essentially at one are of one genus. Now the peculiarly formed follicular pericarp, with its spindle-shaped mass of flat obovate imbricated silky-appendaged seeds, is so exactly one thing throughout all the 1600 or 1800 species of this family that it plays almost no part at all in the delimiting of the genera. Bentham & Hooker, in their elaborate key to the 7 tribes & 146 genera of the order, do not once mention the fruit. It is essentially the same thing in all. And if the synthetic value accorded to pods & seeds in other families were admitted here, instead of nearly 200 genera of Asclepiads we should have scarcely more than the 2 or 3 that were recognized by Tournefort & by Linnaeus.

It was only within the present century that men began to see that, in the treatment of these plants, an exception must be made as to the synthetic value of similarity in fruit. Even as late as about the year 1815, everybody, even the most accomplished systematists, presented the genus *Asclepias* as including not only our types of *Acerates, Asclepiodora, Podostigma & Anantherix*, but also even *Vincetoxicum, Sarcostemma, Oxypetalum, Gonolobus, Enslenia & Hoya*, not to mention the representative species of as many other genera, as the genera of Asclepiads are now understood & accepted.

The complete dismemberment in recent times of the *Asclepias* of the celebrated 18th century and early 19th century authorities—this breaking up of their one genus into a natural family—is doubtless expedient, and must continue to stand approved. But I conceive that the real principles upon which the segregation of genera has proceeded, and may still proceed further, have not been sufficiently looked into.

It is not only in respect to their fruit that *Asclepias* and the many genera that have now been segregated from it are quite alike. They have the same umbelliform inflorescence, the same calyx, the same corolla, the crown only excepted, and they are treated as if [there were] no notable disagreement among themselves even as regards their stamens & pistils.

It is, as I have just intimated, in the corona of the perianth, with its interesting diversities in the minutiae of its conformation, that so many characters of supposed generic value have latterly been detected. To some of these modifications of the corona a fanci-

ful & exagerated importance has been attached; as for example to that diminutive organ which is commonly known as the horn of the hood. It is easy to note the presence or absence of such an organ; and because it is easier than to recognize, or teach to recognize, a difference in habit, therefore even the professed systematist is under a temptation to rely upon it as an essential generic character; to magnify its importance. It was Linnaeus, the most unnatural & artificial of systematists, who indicated the horn of the hood as the character of *Asclepias;* and yet, a hundred years after Linnaeus, men like Bentham & Gray, professedly ignoring artificialism in taxonomy, are more absolute artificialists than Linnaeus himself when they come to the treatment of *Asclepias* and its allies; for they both make the horn the absolute & only mark of *Asclepias,* which Linnaeus, after all, had too much of the sense of what is natural & rational in classification to carry into effect. He does indeed name the horn as a character of the genus, yet, out of his 18 species of *Asclepias,* only 11 have it; the other 7 being destitute of any trace of it. And he did not know one of those plants of the United States now placed, some in *Acerates* and others in *Gomphocarpus* by Bentham and by Gray. It was no wonder, therefore, that all these plants, as well as the types of several other hornless-hooded genera of ours, were early referred by their discoverers to *Asclepias.*

And Elliott, who founded *Acerates,* and who lived & wrote before the revival of the Natural System, did not rely so wholly upon that negative peculiarity of the absence of the horn as the name which he assigned the genus might seem to imply; for he says: "It is perhaps doubtful whether the absence of the horn-like appendages constitutes a sufficient character to establish this genus. I should have been better satisfied with it if it had separated the species of *Asclepias* with alternate, from those with opposite leaves."

If Elliott had proceeded to state what he found in the habit of his *Acerates* to mark it as unlike *Asclepias,* he must needs have mentioned (1) the strictly lateral inflorescence, the umbels being ranged up & down almost the whole length of the stem, yet none being terminal; (2) the sub-sessile character of the umbels; (3) the small size, narrow & elongated configuration, and the green color of the individual flowers, &c. To me these several peculiarities make so stong an impression of the distinctness of the genus that I should have supported its validity if every species of it had been furnished with the "horn" of *Asclepias.* And I am at perfect agreement with Britton in his having transferred the *Asclepias stenophylla* of Gray to *Acerates.* It is simply an *Acerates* with a horn to its hood; just as certain Californian plants of the *Asclepias* habit are of the genus *Asclepias* though completely destitute of the horn.

But there is one point in the floral structure of *Acerates* by which it differs constantly from *Asclepias,* and that is the outline of that curious organ called the anther-wing. This throughout *Acerates* is angled & notched at about the middle, from which point it tapers both ways. In *Asclepias* it is broadest & notched at the very base, thence tapering to the summit. This character was noticed by Gray, though he did not accentuate it, preferring to treat the horn of the hood or its absence as the more important. That he was wrong in this judgment is demonstrated completely by the fact that treating the horn as the more essential technicality he was obliged to ignore habit, and put into *Asclepias* a species which is, as he admitted, habitally an *Acerates.* And to the anther-wing character is necessarily accorded a higher importance because it brings together plants at perfect agreement in habit."

Habitat

Most members of *Asclepias* are grassland plants that grow in full sun. But with 80 or so species spread over a continent it would be unusual if there were no exceptions. Some species grow in woodlands; these include *A. quadrifolia, A. variegata, A. purpurascens, A. cinerea, A. humistrata, A. curtissii, A. exaltata, A. ovalifolia, A. texana, A. angustifolia, A. cordifolia, A. quinquedentata* & *A. hypoleuca*. Many western species like it fairly dry, but several, *A. angustifolia* & *A. mexicana*, like it wet. Several eastern species grow in marshes; *A. incarnata, A. rubra, A. lanceolata, A. connivens, A. viridula, A. perennis* & *A. longifolia*. Bear in mind that these designations are not rigid and individuals of these species will be found outside of these areas. Many grassland species do quite well in partial shade and wetland species, like *A. incarnata*, can grow on drier sites. In Florida & Mississippi *A. amplexicaulis* grows in open woodlands; in Oklahoma & Kansas in grasslands. In Missouri, *A. purpurascens* seems to prefer woodlands & shady roadsides, but it can also be found less frequently in grasslands. In Florida, *A. longifolia* grows in wetlands, in Missouri in prairies. These are adaptable plants; they grow where you find them.

The grassland habitat may be beneficial to many species today with the spread of paved roads, ditching, and the mowing of their roadsides. This mowing creates artificial grasslands that are moistened by runoff from the paving. I have seen many species thriving in these areas, that I did not see elsewhere. The occasional grading of gravel or sandy roads in the arid west creates disturbed soil that is often readily colonized by many of their species.

Many milkweeds grow in sandy, well-drained soils. Some, like *A. arenaria, A. tomentosa, A. erosa, A. ruthiae, A. involucrata* & *A. humistrata* like deep sands, while *A. welshii* is found only on dunes in Utah & Arizona. Even so, many species, especially the eastern ones, do quite well in heavier, wetter soils.

Members of *Asclepias* can be found from sea level to 9000' in the U.S. However, I know of only a single species that grows within most of this entire range, and that is *A. speciosa*; I have seen it near sea level in Los Angeles Co., CA and at 8300' in Mineral Co., CO. *A. hallii* also grows at 8300'and is said to grow to 9000', but it doesn't go below 6000' or so. On the sky islands of S. Arizona, I have seen *A. quinquedentata, A. hypoleuca* & *A. lemmoni* up to about 8000', but no lower than about 6000'. There are a number of western species that grow between 4000' & 6000'. These include *A. macrotis, A. sperryi, A. nummularia, A. elata, A. uncialis, A. ruthiae, A, involucrata, A. macrosperma, A. cutleri, A. cryptoceras*, and possibly *A. brachystephana*. 6000' seems to be a cut-off elevation for many of the species.

The genus is divided pretty well by the Great Plains and only a few species cross it to any extent. In moving from east to west most of the eastern species drop out at about longitude 98° that runs through Ft. Worth, Oklahoma City & Wichita. This is about where the humid tallgrass prairie blends into the sub-

humid shortgrass plains and where the line of 20" equivalent rainfall occurs. Driving along the highways, I saw *A. syriaca* replaced by *A. speciosa*, *A. latifolia* & *A. arenaria*; *A. viridis* replaced by *A. asperula*; *A. stenophylla* & *A. longifolia* replaced by *A. engelmanniana*; *A. verticillata* replaced by *A. subverticillata* & *A. pumila*. However, there are a few species that do cross this line. Most notably, *A. tuberosa* and *A. verticillata* go all the way over to longitude 111° in S. AZ.; *A. viridiflora* goes over to longitude 105° in W. TX & NM; and *A. ovalifolia* to the same longitude in SD & Saskatchewan. From the west, only *A. speciosa* goes over to about longitude 92° in MN.

Habit

All members of *Asclepias* are long-lived perennials (*A. curassavica* is annual in temperate areas). How long they can live has never been established, but here on my farm in central Missouri I know that some of the clumps of *A. tuberosa* are at least 20 years old and that some of the plants of *A. viridiflora* and *A. longifolia* that have been sprouting up from the same locations year after year must be as old. In searching out the plants for this study, I often went to areas cited on herbarium sheets and usually found the species still there if the site had not been disturbed. In a few cases the citations were at least 50 years old, but I found the species still there. I had no way of knowing if any of the plants were the ones the collector had seen, but the colony was still extant.

Milkweeds grow solitary or clustered, with their stems erect or decumbent. The number of stems depends upon the age of the plant, the growing conditions and the species. A young plant will usually have a single stem; an older one will have several to many if growing conditions are good. I have seen single plants of *A. tuberosa* with 60 stems and a thousand flowers; huge plants of *A. albicans* & *A. subulata* with as many. In CO I have seen stunning clusters of *A. asperula* with 50 umbels; in MO of *A. viridis*; in CO of *A. hallii* & *A. speciosa*. But I have never seen *A. viridiflora*, *A. quadrifolia* or A. *variegata* with more than 3 stems from a single plant. *A. cinerea* & *A. feayi* are usually seen solitary, as is *A. rubra*, *A. lanceolata*, *A. viridula* & *A. pedicellata*, though I have seen a few with several stems. The decumbent species often form rosettes as they mature. Old plants of *A. involucrata*, *A. macrosperma* & *A. humistrata* form beautiful rosettes. The erect and decumbent habits are not mutually exclusive, but can be found within the same species. Though normally erect, *A. viridiflora* is often found decumbent in the westernmost part of its range on the high plains. Normally decumbent, *A. ruthiae* & *A. uncialis* do rarely show erect forms. *A. viridis* is usually decumbent in much of its range, but is usually erect in TX. *A. asperula* is usually decumbent in the easternmost part of its range, but becomes erect in CO, TX, NM & AZ.

Many milkweeds have their leaves arranged in a decussate manner, especially the taller species. In two species, *A. humistrata* & *A. rubra*, the stem twists 90° to put the leaves in one plane. Yet others have them arranged in whorls or irregularly around the stem. Many have broad leaves, others have very narrow ones. On some they are thick & leathery; on others thin & papery. They may be glabrous or wooly; petiolate or sessile. But one feature that they all have is their entire margins, and these margins are often undulate. In some species (notably *A. viridiflora, A. arenaria, A. curtissii, A. meadii* and *A. welshii*) there is an extreme dimorphism in the leaves, with those of the young plants having filiform leaves and those of the mature plants having much broader ones. *A. viridiflora* shows the greatest diversity of leaf form and habit of any species within the genus (see photos).

On the stems of many milkweed species there are narrow lines of fine hairs. These lines begin in the axils of the leaves and go up the stem to end at the interpetiolar space of the next node. Plants with opposite leaves will have two of these lines, but those with whorled leaves may have as many as 5 or 6 depending on the number of leaves in the whorl.

Milkweeds vary greatly in size. If the colony of *A. syriaca* on my farm, which last year had over 100 stems, is a single clone, that would likely make it the largest species within the genus. The largest single plant cluster that I've seen, in which all of the stems come from a tight center, was one of *A. albicans* that I saw in AZ that was about 8' tall and just as wide with very many stems and several thousand flowers. The smallest was a single blooming stem of *A. uncialis* that was only 1" or so long, and an equally small plant of *A. ruthiae.* With these latter two, however, it is only a guess if one is viewing a single plant or a shoot from a larger plant, since plants a foot or more apart have been shown to be joined underground. In 2006 **Karin Decker** dug up some plants in CO and provided photographs of their rooting habit. Which brings up a point.

On page 3 **Woodson** stated, "I know of no truly rhizomatous species, but some, as *A. syriaca*, may produce gemmiferous roots giving rise to clones of limited extent." I was skeptical of this statement because 1) I knew that Woodson had not examined the roots of every species; 2) I could not find his term, "gemmiferous roots", in any botany text and wondered if he had coined it himself; 3) in cultivating various species, I had observed *A. syriaca, A. speciosa,* and *A. sullivantii* spreading from their initial plantings and producing clones of themselves by what I presumed to be rhizomes (underground stems); I had also noticed clones of *A. amplexicaulis* in the field; and 4) I had read of other authors referring to rhizomes in *Asclepias.* In 1938 **Mayberry** described *A. pumila* as "perennial by a slender elongated rhizome" and "The rhizome of *A. quadrifolia* is relatively short & thickened. [Their roots] are finely branched and emerge all along the extended rhizome." In 1984 **Bookman** wrote of using 6" pieces of *A. speciosa* rhizome to propagate it. Consequently, I dug down about 4" and exposed a portion of the horizontal root/rhizome of *A. syriaca* on my farm and cut out a small piece of it to examine beneath a microscope. The piece I removed

was 6—7 mm in diam., whitish & smooth, with several fibrous roots emerging from it. To my surprise, it was not a rhizome, but a storage root similar in x-section to a small sweet potato root, with the cortical and parenchyma cells packed with starch grains. Later, I acquired similar pieces from *A. sullivantii* and *A. welshii* and came to the same conclusion: they were roots, not stems. These species send out roots horizontally about 3—6" beneath the ground, and these produce sprouts at intervals. To date I have found nothing that refutes Woodson's statement. The term 'rhizome' in *Asclepias* has been misused.

Since all members of *Asclepias* are long-lived perennials, most of which die back seasonally, it follows that they develop some form of storage root to tide them over. I didn't go about digging up plants, so I can't say what all of their roots are like, but I have seen some in illustrations and in photos on the internet by folks who did do some digging. Many species have thickened roots like heavy cord or even like rope; these include *A. quadrifolia, A. macrotis, A. uncialis, A. ruthiae & A. tuberosa.* Others have thickened roots much like those of ginseng, and include *A. viridis* and *A. oenotheroides.* While *A. incarnata, A. verticillata* and *A. longifolia* have thick coarse roots like onions.

The inflorescence may be terminal or lateral. Some of those with lateral ones may go on producing new umbels as the shoot elongates, blooming for several months under good conditions and producing hundreds or even thousands of flowers, as in the case of *A. incarnata, A. verticillata, A. curassavica* or *A. tuberosa.* Those with terminal umbels may produce as few as 3—4 flowers on a single plant, as in *A. cinerea & A. feayi,* and the blooming period be as short as a week. Some of the species with terminal umbels produce multiple stems in rosettes or clusters. In UT I have seen rosettes of *A. involucrata* with as many as 14 terminal umbels. In CO I have seen clusters of *A. asperula* with over 50 terminal umbels.

Members of *Asclepias* divide fairly nicely into spring bloomers and summer bloomers. The former are generally small plants (*A. uncialis, A. nummularia, A. involucrata*), but a few are larger (*A. quadrifolia, A. cryptoceras* and *A. viridis*). But what they all share is a very early development of the flower buds. When their shoots emerge from the ground, their flower buds are easily seen at the apex of the shoot. In a few cases I have seen nearly mature buds and even open flowers emerging from the sand (*A. cryptoceras* and *A. ruthiae*). Spring bloomers mostly have terminal umbels and often lateral ones as well close behind the terminal ones. By contrast, summer bloomers are large plants with the flowers developing weeks after the shoot emerges from the ground. The umbels may be terminal or lateral. The earliest bloomers in Missouri are *A. quadrifolia* and *A. viridis* (mid-May). They are followed by *A. amplexicaulis* and *A. meadii* (late-May), *A. tuberosa* (early June), *A. syriaca* and *A. purpurascens* (June), *A. viridiflora* (July) and *A. incarnata* (late July).

Flower

The milkweed flower is unique among dicotyledonous plants, and for this reason it has taken botanists a very long time to completely understand its very complex structure. This is not to imply that they were all working on it day & night during this period, but those who did study it made assumptions that delayed our understanding of it. As I mentioned, the European milkweed, now *Vincetoxicum officinale*, has been known since ancient times as a medicinal plant. However, its flower is fairly small and the sexual parts even smaller, so that it required the invention of the lens even to get a good look at it. Even so, when **Linnaeus** first placed it in *Asclepias* along side other species with much larger flowers, no one at the time was even certain how many stamens it actually had. **Linnaeus** made the educated guess that the number was 5 because the remainder of the flower was 5-merous, i.e., it had 5 sepals, 5 petals, 5 corona lobes, 5 appendages atop the stigma and 5 glands. Even so, it could still have had 10 stamens and many of the best botanists of the time thought it did. They interpreted the translator arms as filaments originating at the glands, with the 10 pollinia as 10 anthers. They maintained that a pollinating oil moved up the translator arms, into the glands and then into the stigma and down the styles. Or, some held that the pollinia germinated in place and the pollen tubes grew into the stigma. In 1793 the German floral biologist, **Christian Konrad Sprengel**, working with then *A. fruticosa*, showed that the glands were devices for catching insect legs and that the insects then removed the pollinia from the 5 anthers and placed them atop the stigma of the same flower. **Sprengel** *assumed* that the flowers were self-pollinated, or he would have recognized this as a mechanism to achieve cross-pollination. His work was not well received and his view was considered fanciful until later discoveries vindicated him.

Part of the problem in interpreting the Asclepias flower was due to examining only the mature open ones. In 1811 the renowned English botanist, **Robert Brown**, published an account after having examined immature, unopened buds and observing when and how these odd structures developed. He discovered that there were 5 two-chambered anthers and that the glands and translator arms were secreted by the stigma. Later in 1831 he was able to show how the pollinia germinated within the stigmatic chambers and fertilized the ovules. Even so, it took several decades before his discoveries were commonly accepted by other botanists.

The most persistant assumption was that the hoods were the nectaries of the flower even though no one could find glandular tissue within them. Nectar was apparent within the hoods, so everyone simply *assumed* that it originated there. In 1886 the Swiss botanist, **Salomon Stadler** examined the *A. cornuti* [now *A. syriaca*] flower anatomically and discovered glandular tissue on the lower surface of the stigma directly behind the stigmatic chambers. This made good sense because the pollen required a sugar solution for germination. **Stadler** found no glandular tissue within the the hoods, but he also noticed a structure

that he called a "saftdecke" or "nectar cover" just below the guide rails (anther wings) and a channel leading from the stigmatic chamber to the hood. Unfortunately he did not follow through on his discoveries. As a consequence, it was long believed that the Asclepias flower had two nectaries, one (5-parted) on the stigma and another (also 5-parted) in each of the hoods. In 1954 **Woodson** stated on page 10, "The hoods are nectaries and provide the attraction for the insect visitors. The papillate cells which secrete the nectar are found chiefly toward the base of the horn." On page 16 he refers to "the abundant nectar which is secreted by the hoods of their coronas." He did not seem to have been aware of **Stadler's** book even though it was in the MBG library where he worked. On page 18 he found it interesting that the "stigmatic chambers are obviously filled with a fluid resembling the nectar of the corona hoods." He, like **Stadler**, had come so close.

In 1965 two Israeli botanists, **Jacob Galil**, founder of the botany department & botanical garden at Tel Aviv Univ., **& Moshe Zeroni**, undertook to re-examine **ler's** work. In doing so, they confirmed that the *Asclepias* flower has only the single, 5-parted nectary of the stigma, and that the nectar moves down the stigmatic chambers to the nectar covers whence it is diverted right & left along tiny channels to the hoods, which function solely as nectar reservoirs. I include here their diagram, to which I have made some corrections. Their paper is in *Botanical Gazette*, Vol. 126. Oddly, they refer to **Stadler's** nectar cover only as a fleshy pad, a most inadequate term, and in the Figures below they use flap [!] in referring to the anther wings.

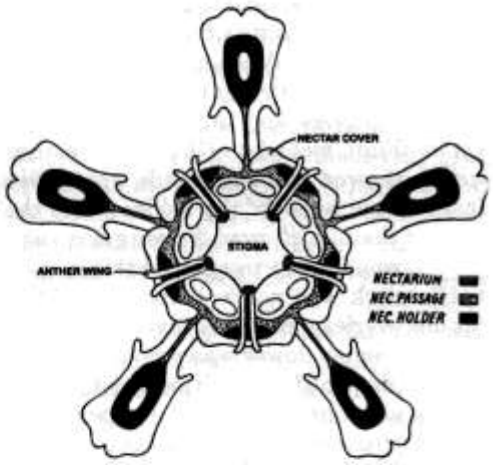
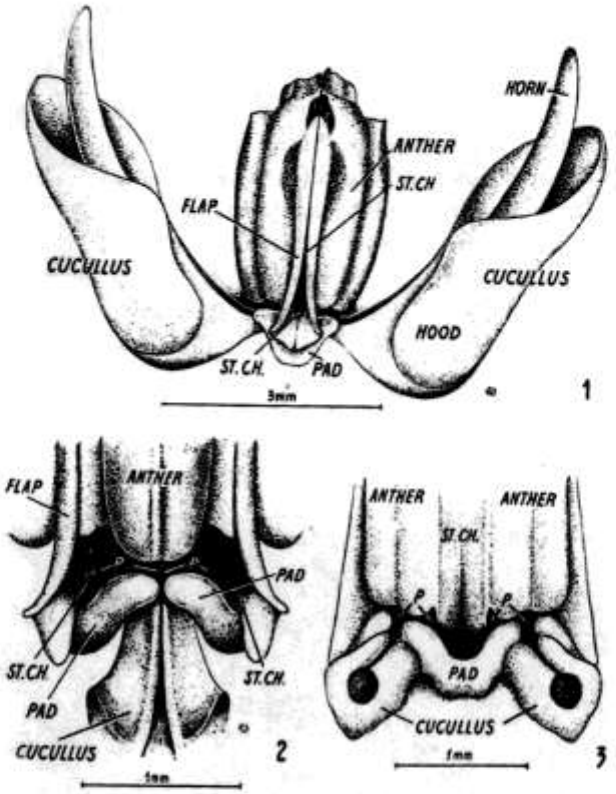


FIG. 10.—Diagram of nectar system of *Asclepias curassavica*, showing nectaria, nectar-holders, and passages between them.



Figs. 1-3. Parts of flower of *Asclepias curassavica*. Fig. 1, part of gynostegium; face view of stigmatic chamber and fleshy pad. Fig. 2, face view of anther and cucullus at their bases; passages from stigmatic chambers from both sides into cucullus in center. Fig. 3, face view of stigmatic chamber at its base; walls have been removed and cuculli cut near their bases; passages from stigmatic chamber to cuculli occur on both sides.

Another plate from **Galil & Zeroni's** 1965 paper that shows important details of the milkweed nectar system.