Trichocereus as a Potential Nursery Crop in Southern Arizona, With Discussion of the Opuntia Borer (Cerambycidae: *Moneilema gigas*) as a Serious Threat to its Cultivation

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Abstract

Southern Arizona and southern California are economically competing regions with regard to production of ornamental cacti and succulents for sale throughout the United States. Economics of field-production vs greenhouse-production are discussed for both regions. Comparatively few cacti and succulents are field-produced in Arizona because few ornamental selections have been located which can economically be produced in the open considering the rigors of the desert environment. The Golden Torch Cactus (*Trichocereus spachianus* (Lem.) Ricc.) represents a promising nursery crop for field production in southern Arizona but has four seemingly unrelated problems. These problems are all shown to result from damage to *Trichocereus* by a single species of Cerambycid beetle, with damage to the cactus occurring throughout the life cycle of the beetle. Despite such an intimate relationship between beetle and *Trichocereus*, and although the beetle seems more destructive to *Trichocereus* than to native North American cacti, the beetle, far from proving to be an Argentinian introduction like *Trichocereus*, actually belongs to the genus of native Opuntia Borer (*Moneilema*), associated with Cholla and Prickly Pear in North America since the classic observations by Thomas Say on Major Long's 1819-20 expedition to the Rocky Mountains. Although the present article is thought to be the first report of damage to *Trichocereus* by *Moneilema*, the degree to which we have found *Trichocereus* in Arizona to be infested suggests a rather long-standing condition. Specifically, we report *Moneilema gigas* LeConte to cause the following pathologic conditions in *Trichocereus spachianus* in Arizona: 1) bacterial and fungal rot of deep internal tissues, 2) external chewing disfiguration by adult beetles, 3) sporadic growth spurts making disfiguring constrictions of the stem, and 4) hollowing out of stems by boring larvae. Possible reasons for the virulence of *Moneilema gigas* in attacking *Trichocereus* are discussed. With the knowledge that four major problems associated with *Trichocereus* cultivation in Arizona actually result from infestation by a single beetle species, and with the possibility of controlling this insect pest, commercial field-production of the cactus in southern Arizona may finally prove economically rewarding.

Preliminary Considerations

Cacti for ornamental use are field-grown and greenhouse grown in southern parts of California and Arizona in large numbers. Large wholesale operations in these warmer states constantly feed bare-root material to greenhouses throughout the United States and Canada where the plants are quickly potted and sold at either retail or wholesale. Arizona, thought of almost universally as a land of many beautiful cacti, nevertheless lags far behind California in commercial production of field-grown cacti. A large number of native cacti are quite legally dug up in nature in Arizona, however, and sold. These native-grown plants are in reality the few "survivors" out of millions of seedling cacti, most of which perished in the desert. If "mother nature" were to charge us a realistic price for digging up her "survivors" we could rarely afford them. In actuality, legislation has indeed made the "survivors" more expensive by requiring the purchase of a separate permit for each "survivor" that must be moved. Although these "survivors" are used for landscaping purposes in Arizona, they are ill-suited to being handled and sold as ornamentals by the thousands of nurseries and greenhouses throughout the United States.

In reality there are severe problems relating to commercial production of cacti in the open in Arizona. The Golden Torch Cactus (*Trichocereus spachianus* (Lem.) Ricc.) of Argentina, however, seems better suited to commercial production in the open in Arizona than in California, except for a series of problems which we now suggest are simply different manifestations of damage by a single insect species. With this knowledge, and with the possibility of controlling the insect, *Trichocereus* might finally fulfill its potential as a nursery field-crop in Arizona. A comparison of the economics of growing cacti in southern Arizona and southern California relates to climate considerations and to whether or not greenhouses are used. There are four basic categories of production: 1) use of greenhouses in Arizona, 2) use of greenhouses in milder southern California climates, 3) field production in Arizona, and 4) field production in milder southern California climates. The value of *Trichocereus* relates in large part to the possibility of it being adapted to category number 3), which is at present poorly developed. A comparison of the economics of cactus production under various circumstances is presented below.

Economic Considerations Relating to Cactus and Succulent Production

Growing cacti and succulents in greenhouses in Arizona requires considerably less energy for winter heating than either 1) growing similar crops in colder climates, or 2) growing non-CAM plants in Arizona greenhouses. This is largely due to the fact that winter heating of greenhouses containing cacti and succulents can be minimal and is more or less to avoid freezing. High night-time temperatures are not appropriate for CAM (crassulacean acid metabolism) plants. Also, the high proportion of sunny winter days in Arizona ensures that greenhouse CAM plants will have a good season of active, healthy growth from November through March.

A major drawback to traditional (non-CAM) commercial greenhouse operation in Arizona is the expense of summer cooling. CAM plants, however, can function at much higher daytime temperatures than traditional greenhouse crops, although cool night-time temperatures and adequate air circulation are essential for good carbon dioxide uptake. As the fiberglass of greenhouses in Arizona ages to become more opaque, CAM crops grow a little better in summer but poorer in winter. Using a sheet-plastic skin for a greenhouse in winter to be replaced by a shade-cloth skin in summer is very effective because it allows better penetration of sunlight in winter and better air movement in summer. The repeated putting up and taking down, however, requires considerable time and storage facilities. Torn sheet-goods require frequent replacement. Perhaps more importantly, the grower takes a chance that the time chosen for the annual change-over will later prove to have been incorrect according to the weather that eventually occurred. A change to shade-cloth at the end of February could prove disastrous if a major freeze occurred in March. Nevertheless a March might be so hot and sunny as to be extremely stressful in a closed house for even CAM plants.

In comparing CAM crop production in Arizona and California, energy use for greenhouse heating and cooling is less in some parts of California due to milder winters and less intense summers. Plant quality, however, of many CAM plants, as measured by color, sheen, spination, and over-all beauty, is often much higher in Arizona-grown material because of more adequate sunlight and lower humidity, and we suspect in some cases because of more adequate aeration at night. Nevertheless some CAM plants such as *Haworthia* and *Euphorbia* produce high-quality plants under California greenhouse conditons. Other CAM species can achieve excellent quality when field-grown in California because of the better quality of sunlight and aeration outside of the greenhouse. Drawbacks include 1) potential damage by excess moisture, rainfall, flooding, 2) growth of bacteria and fungi encouraged by dew, fog and humidity, 3) possible sunburn on days when fog, clouds and humidity are gone (e.g. when Santa Ana winds blow in off of the desert) unless plants have already been "broken in" to the sun, 4) freeze damage in some locations.

Although the production of ornamental cacti and succulents on a commercial crop basis is still centered in California's southland, particularly around Vista in northern San Diego County, there is significant production of Medicinal Aloe (*Aloe vera*) in Texas and Golden Barrel Cactus (*Echinocactus grusonii*) in Arizona. Most cactus and succulent production in Arizona, however, is in greenhouses to protect young seedlings from freezing temperatures in winter and to allow diffusion of light to minimize "sunburn" in summer.

The region around Vista in southern California is rather unique in the United States for its combination of 1) low background incidence of freezing weather, 2) presence of topography with many slopes which face the sun on winter days and which allow freeze-bearing air to drain away on winter nights, 3) maritime influence of humidity to partially diffuse the sun's rays to reduce "sunburning" of cacti, particularly in summer, 4) position far enough inland from the seacoast itself so there is relatively more sun and less fog, and 5) low rainfall. Under the above rather unique combination of conditions, many ornamental cacti and succulent species can be economically grown in fields. Further, the expense of maintaining greenhouses for propagation, and for production of fine unblemished specimens, is relatively low due to little or no heating costs in winter and little or no cooling costs in summer.

With increasing energy costs in Arizona, and with other costs of building and maintaining fiberglass or sheet-plastic greenhouses, an old question reasserts itself:—why can't more types of cacti be economically grown in the open in Arizona? The first two of the drawbacks listed as negative factors for outdoor cactus growth in California would be of less importance in Arizona, but the second two would be of much greater importance.

Although at first glance it might appear that cacti grow anywhere in the open in the Arizona desert, in actuality only a few seedlings of Saguaro (*Carnegiea gigantea*), for example, out of many millions of seeds, grow and prosper under the protecting branches of "nurse plants" which shield the tender creatures from frost and intense sun until they grow older and become "broken in" to the harsh desert environment over a period of many years! Nevertheless, there are indeed cacti, notably some from Argentina, which seem to thrive on intense sun and heat of summer but are yet relatively resistant to freeze-damage in winter.

The Golden Torch Cactus (*Trichocereus spachianus*) of Argentina has been identified as a potential crop plant for nursery production in Arizona. When sun-grown in fields in Arizona *T. spachianus* makes beautiful golden organ-pipe-shaped plants three or four feet tall with 5-10 erect columnar stems. These clumps can be sold as specimen plants for landscaping or can be used as "cutting stock" for the production of 4-inch or 6-inch (pot size) columnar cacti

Adults of Moneilema gigas *on Prickly Pear (*Opuntia phaeacantha*) near the Boyce Thompson Southwestern Arboretum. Prior and partially healed damage to both fruits and stem due to chewing by* Moneilema *is evident. Photo by Carol D. Crosswhite, August, 1973.*

Stems of Trichocereus spachianus *in infested gardens become multiply-segmented due to repeated cycles of destruction of apical meristems by* Moneilema *adults. As each new growing apex is destroyed, a lateral bud at the edge of the eaten area is released physiologically from dormancy to produce a new branch atop the old, making a prominent constriction. Photo by Carol D. Crosswhite, February, 1986.*

Details of Trichocereus *disfiguration by* Moneilema. *This stem shows destruction of the apical meristem by adult beetles and the incipient budding off of a new head at the edge of the chewed top. The lateral chew marks farther down were made by an adult which positioned itself head down and vertically. Photo by Carol D. Crosswhite, February, 1986.*

for ornamental use.

The market potential for these latter pot plants is great because they can be economically shipped to retail nurseries throughout the United States bare-root and stacked like cord-wood in boxes. By growing *Trichocereus* as large outdoor plants for cutting stock, the critical seedling stage which is highly susceptible to damage by frost and sunburn is eliminated. Formation of adventitious roots by *Trichocereus* cuttings is excellent; for Saguaro very poor.

When *Trichocereus spachianus* is grown in fields in the Vista region, it lacks the healthy, shiny, golden and elegantly spined appearance it has when grown in the Arizona desert using suitable horticultural care. The higher humidity in the Vista region seems to allow microorganisms, particularly a chlorophyll-obliterating or -obscuring fungus, to invade the surface and outer subsurface of the plant. The same disfiguration often occurs if a *T. spachianus* plant is greenhouse grown in Arizona or elsewhere for a long period of time. When *T. spachianus* is grown under field conditions in the desert of southern Arizona the malady is greatly minimized and the loss of chlorophyll from old stems is greatly slowed, although perhaps never eliminated since it appears almost to be part of the natural aging process of the species. Since the "aging" or loss of chlorophyll proceeds very slowly from the base of the plant upwards with time, and since the plant is a rapid grower, the apical stem tips which are taken as cuttings are always extremely healthy, vigorous and free from microflora in Arizona. Thus, if there were no other factors, *Trichocereus* as a nursery field crop would be much more successful in Arizona than California.

Nevertheless, cultivation of *T. spachianus* has had only spotty success as a crop in Arizona and stands of the plant tend to decline over time. Poor success has been attributed to four seemingly distinct problems: 1) bacterial and fungal rot of deep internal tissues, 2) external chewing disfiguration by insects, 3) sporadic growth spurts making disfiguring constrictions of the stems, and 4) hollowing out of stems by boring insects. The present article attempts to demonstrate that all four of these serious problems are actually a result of transference of a pest of native Arizona Cholla and Prickly Pear to the Argentinian *Trichocereus*. We see the Opuntia Borer (Cerambycidae: *Moneilema gigas* LeConte) as the ultimate cause of all four types of damage and characterize it as a serious threat to *Trichocereus* cultivation in Arizona unless adequate control measures are taken.

The Opuntia Borer

Science first became aware of a peculiar group of large, black, flightless, nocturnal, cactus-eating beetles when Thomas Say discovered the first species on Major Stephen H. Long's 1819–20 expedition to the Rocky Mountains. Following the Louisiana Purchase and the War of 1812, John C. Calhoun, Secretary of War, had ordered the expedition into the field to explore the western territory or "Missouri Country" as it was then known. This was popularly known as the "Yellowstone Expedition" at the time although it never did come close to what is now Yellowstone National Park. The expedition was charged with recording "*every thing interesting in relation to soil . . . and productions, whether animal, vegetable or mineral . . .*" in the vast, largely unknown territory of the west. The agreement with Britain had just been concluded which would set the northern boundary of the United States on the 49th Parallel "*. . . to the summit of the Stony Mountains.*"

Say (1824) described the cactus beetles which he discovered on this historic expediton not only as representing a new species, but an entirely new genus, *Moneilema*. The genus is now known to comprise at least six good species, although many more have been named, for example by Dr. Psota (1930) before he was gunned down in mob warfare. All species of *Moneilema* are large, black, nocturnal, flightless beetles which feed apparently exclusively on cacti. The genus is now considered so distinct within the family Cerambycidae that it is treated as comprising a monotypic and wholly North American tribe, the Moneilemini. The genus has occasionally been compared with Old World flightless Cerambycids such as *Dorcadion* and *Parmena* but its referral to either tribe Dorcadionini or tribe Parmenini by authors was thought by the most recent monographers to have been on superficial characters: "*Loss of wings and associated anatomical modification which result in convergence among Cerambycidae, appear to represent response to special environmental conditions, such as root feeding, subterranean habits, arid regions, insular existence, and other situations where flightlessness favors survival.*" (**Linsley and Chemsak, 1984: p. 18**).

The species of Opuntia Borer which Say described in 1824 was *Moneilema annulata*, about 16 mm long. It feeds on Prickly Pear (*Opuntia polyacantha, O. phaeacantha*). The species which attacks *Trichocereus* in Arizona, *Moneilema gigas*, has the largest adults in the genus, about 27 mm long. Linsley and Chemsak (1984), in the most up-to-date and thorough monograph on this group of Cerambycidae, give *Opuntia fulgida* and *Opuntia "leptophylla"* as the normal hosts of *Moneilema gigas*. Although we agree that *Opuntia fulgida* (Chain-Fruit Cholla) is indeed an important food plant, the identity of "*O. leptophylla*" is indecipherable. Perhaps *O. leptocaulis* was intended. If so, both species cited would be chollas.

We find chollas and prickly pears to both be eaten regularly by *M. gigas*, particularly the cholla *Opuntia fulgida* and the prickly pear *Opuntia phaeacantha* (="*O. engelmannii*"). From our examination of 165 pinned *M. gigas* specimens in the insect collections of the University of Arizona at Tucson and Arizona State University at Tempe, it is clear that both Cholla and Prickly Pear are regular food. There is also a record of the club-stemmed *Opuntia stanlyi* being eaten (W. L. Nutting, x-13-1957, Aravaipa Canyon, Pinal County) and of a planted 7-inch Saguaro being killed at Saguaro National Monument by the beetles (S. A. Alcorn, iv-20-1967).

Adults in collections were generally collected from mid-April to late November, although L. P. Webrie (cf. Univ. of Ariz. insect collection) collected the species in Tucson on February 4, 1939. In mid-February, 1986, we observed fresh *Moneilema* chew marks on a single *Trichocereus* stem, although such off-season chewing had not been observed in previous years. When Mann (1969) kept adults of *Moneilema gigas* from Arizona in cages in

Uvalde, Texas, some overwintered and the last individual died in late April, a proven longevity of 9.5 months. Since there is a significant gap between the February 4 beetles of Webrie (which can be assumed to be overwintering adults near death) and the sudden appearance of the species in strong numbers beginning the second week in April, this latter period must certainly mark the beginning of emergence of new adults from the pupal chamber. Mann (1969) treated emergence in Arizona as beginning in May and reaching its height in July. The greatest number of pinned specimens in collections were taken in July and August. We interpret specimens collected from September through November as being previously emerged individuals. Mann (1969) determined that eggs were normally laid from June to August. Caged individuals continued feeding into December but stopped egg-laying by mid-August. A secondary peak of pinned specimens in collections taken in October almost matches the numbers of pinned specimens for July or August. We interpret this peak as probably due to student collecting of post-prime adults for required specimens for course work.

The following observations result from our study of *Moneilema gigas* in relation to *Trichocereus spachianus* in southern Arizona, principally Pinal County.

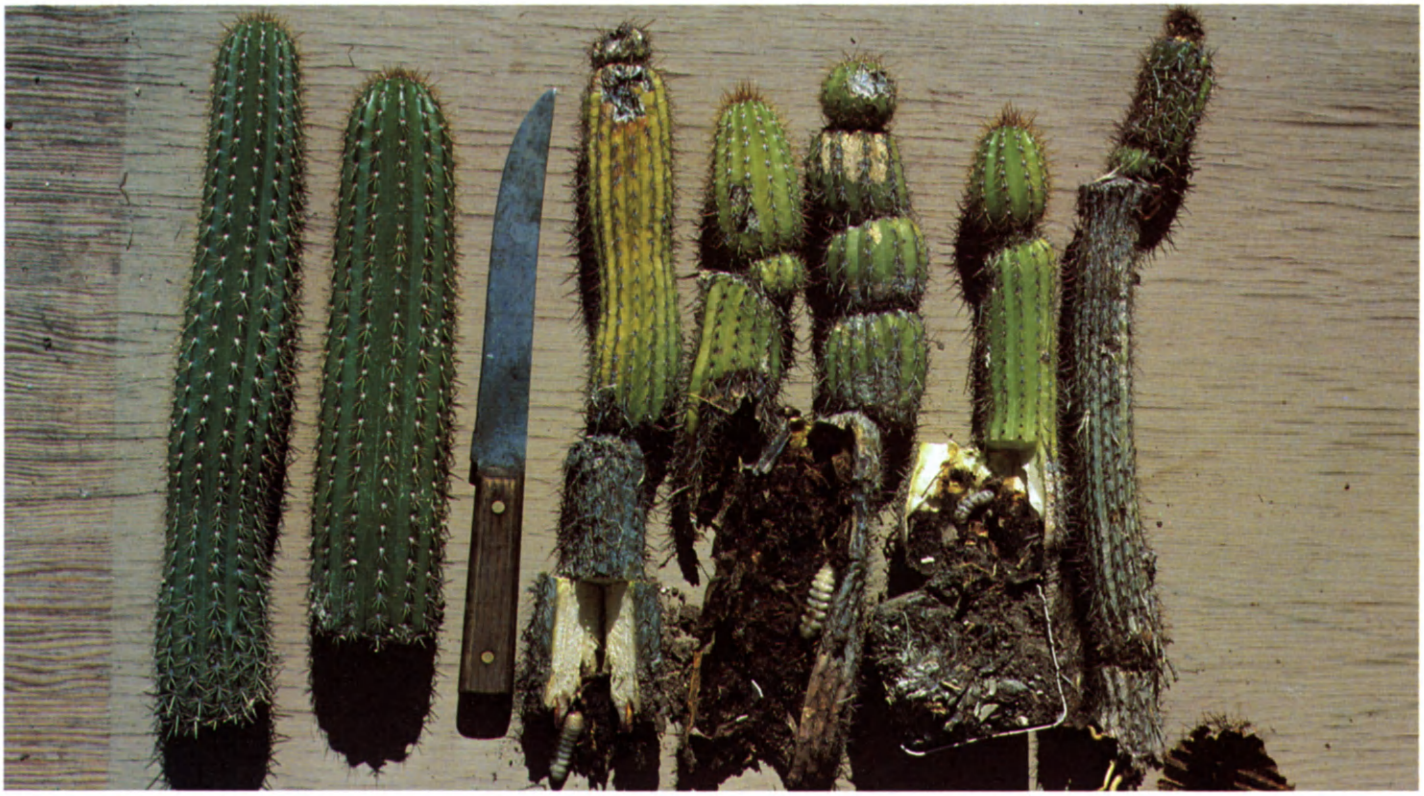
Feeding Stance of the Adult. The adult ascends the stem of *Trichocereus spachianus* at night usually to the apical meristem at the very top. In this area of new growth the tissues are juvenile, i.e. rich in sugar, mineral nutrients, and moisture, but relatively unthickened, unhardened, and still relatively low in stored by-products of metabolism which might act as antifeedants. Although the beetle can feed in a variety of positions, it eventually assumes an attitude of head pointing downward and abdomen upward, very similar to the stance of the Pinacate Beetle (Tenebrionidae: *Eleodes* spp.), also large, black and flightless. The adult of *Moneilema gigas* is positioned in this attitude from midnight onward, slowly chewing on a single *Trichocereus* stem as if a complicated digestion was necessary, and can sometimes be seen at dawn still on the cactus, almost motionless in this characteristic abdomen-elevated attitude.

We interpret the relatively large size of the adult of *M. gigas* together with head-down, abdomen-up attitude as making it a superficial mimic of *Eleodes*. This latter genus of Tenebrionid emits a very foul substance which makes it extremely unpalatable to predators. *Moneilema gigas* is particularly susceptible to predation at dawn when about through feeding but practically in arrested motion as if its meal were digesting. Although *Eleodes* would not be found at the top of a *Trichocereus* cactus at dawn, a predator which had tasted the awful chemistry of *Eleodes* would not know this and would probably treat a *Moneilema* as if it were an *Eleodes*.

Disfiguring Segmentation of the Trichocereus Stem. The most striking feature of mature plants of *Trichocereus spachianus* in Arizona is the common failure of stems to continue growing at an acceptable rate. From the constrictions of the stem it is obvious that growth has completely stopped, often many times through the life of the plant, with new growth coming only from new buds. What has killed the apical meristem? Often meristem death has been

A male Moneilema gigas *has approached and positioned its body parallel to that of a feeding adult female, preparatory to mating. The female was feeding in the head-down vertical position shown, a common stance assumed by adults when feeding on ribbed portions of the cactus below the apical meristem. The characteristic gray segments on the antennae are particularly noticeable on the female in this view. Photo by Carol D. Crosswhite, August, 1983.*

A mated pair of Moneilema gigas *in copula atop* Trichocereus spachianus. *The cactus shows old and partially healed complete destruction of the apical meristematic region and recent chewing by* Moneilema *slightly lower. The stout thoracic spine which shows in profile on the male is a characteristic of* M. gigas. *Photo by Carol D. Crosswhite, August, 1983.*



Five infected stems of Trichocereus spachianus *are shown to the right of the butcher knife, with two healthy stems to the left. Larvae of various instars are visible among the frass and necrotic tissues of three of the infested stems. Most infested stems also show external chewing by adults and pronounced constrictions between growth segments due to repeated destruction of apical meristems by the beetles. Stems infested with larvae lose their original healthy green coloration as destruction of the vascular system below prevents uptake of water and nutrients. Infested branches break off or bend down and become sunburned because of the unfavorable angle in relation to the rays of the sun. The branch at extreme right shows new adventitious roots at the base indicating a first stage of rejuvenation in the plant following pupation of the larva and emergence of the adult, but new chewing marks at the apical meristem indicate perhaps a loosing battle. The butcher knife is approximately 12 inches long. Photo by Carol D. Crosswhite, February, 1986.*

assumed to be due to freezing weather and has wrongly given the species a frost-tender reputation. Indeed, many columnar cacti cultivated in Arizona do display stem constrictions due to winter freezing. Our studies indicate, however, that the apical meristem of *T. spachianus* is killed in summer rather than winter and that death is due to feeding by adults of *Moneilema gigas*. Unless the cacti are checked between midnight and dawn in the summer, the agent of destruction will not be found.

Loss of Chlorophyll. The hallmark of a *Trichocereus* plant infested with larval *Moneilema gigas* is the loss of chlorophyll in the lower part of the stem. Infested plants are easily picked out of large blocks of nursery-grown *Trichocereus* by the tell-tale yellowed stems in winter. We have not yet found a yellowed *Trichocereus* stem in January through March which did not contain a larva of *Moneilema gigas*. We have found only one larva per yellowed stem and have never found a larva in a stem still green from January through March. The unfailing and conspicuous loss of chlorophyll in winter provides a screening process to ensure that infested plants are not sold. Any yellowed stem should be opened with a knife and the larva killed, since merely discarding the yellowed plant will result in pupation of the larva, followed by emergence and breeding. Loss of chlorophyll in the infested stem appears to result from the action of microorganisms introduced by the larvae.

Deposition of Eggs and Early Larval Development. The adult female deposits eggs at ground level of the *Trichocereus* in litter where the very young larvae will be shaded. The tiny larva chews at the base of the cactus and introduces microorganisms which soften the tissues so that exudate is produced. Although such an exudate in *Opuntia* has been described as a defense by the plant, we see the exudate of *Trichocereus* as nourishing the small larva until it is strong enough to gain a foothold within the stem.

Microorganism of Mandibles, Gut and Frass. Larval infestation of *Trichocereus* results in a large hollowed-out cavity in the stem with several colors and textures of decaying tissue and frass. The fresh areas of pulpy tissue which have been recently chewed against by the mandibles of the larva have a yellowish orange patina, obviously surface-colonies of microorganisms. Sectioning beyond the

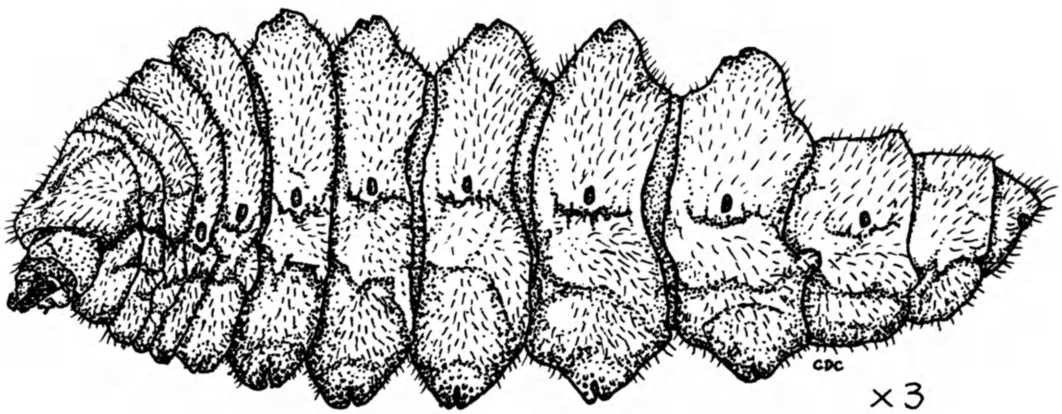
Late instar larva of Moneilema gigas *within a stem of* Trichocereus spachianus. *Note the extensive necrotization of the cactus with larval frass, wound exudate, and rotting tissue. The legless larva moves by lengthening and shortening its body, thus extending and retracting the body segments, each of which is then appendage-like in function. The larva chews into fresh cactus tissue with powerful mandibles (dark-colored) which are the most prominent features on the small head (left). Much of the larva's internal anatomy can be seen through the translucent integument. Photo by Carol D. Crosswhite, February, 1986.*

Opposite page (left)

Trichocereus spachianus *infested with an early instar larva of* Moneilema gigas. *The adult beetle does not lay its eggs within the cactus. Rather, eggs are deposited at soil level and the young larvae chew their way into the plants. Note the entrance hole for this larva at lower left and the already extensive cavity with frass and rotting tissue at the base of the plant. The necrotic region (dark-colored) contrasts sharply with the light-colored healthy tissue above. Bacterial and fungal pathogens in the gut and on the exterior of the larvae invade the succulent parts of the cactus and seem to break down the tissues for easier digestion by the larvae. Note the yellowish streaks extending upward to the healthy portions of the cactus, indicating infection of the tissues in advance of the chewing.*

Opposite page (right)

The canal-like chamber beneath this Moneilema *larva leads from the feeding area within the plant down to the root region where a pupal chamber has been constructed. When the last instar larva is fully grown, it retreats to this chamber, pupates, and finally emerges and digs its way through the soil as an adult beetle. Exit holes in the soil can sometimes be noted in a colony of infested* Trichocereus *by their characteristic diameter which matches the diameter of the beetle, and by their rounded nature which also matches the rounded body of the adult beetle. The rounding of the holes is thought to be due to re-use, the old pupal chambers serving as refugia from the midday heat for the beetles which emerged from them. Photo by Carol D. Crosswhite, February, 1986.*



Larva of Moneilema gigas. *Drawing by Carol D. Crosswhite, April, 1986.*

chewed areas, we find yellowish streaks of infection radiating into healthy soft tissue. The infectious streaks of low-grade necrotization invading otherwise healthy tissue are interpreted by us to indicate that the microorganism is weakly pathogenic for *Trichocereus*. Behind the advancing wave of infection is the larva itself and a conspicuous area of microorganism-rich dark-colored frass and purulent exudate. The areas recently chewed by the mandibles appear to have been softened by the microorganism slightly in advance of the approach of the larva itself. We interpret the weak pathogen as being repeatedly inoculated into fresh tissues on all sides of the cavity through the chewing activity of the mandibles. As the larva methodically works its way around the perimeter of the cavity, chewing at the edges, it consumes the tissue which we interpret as "conditioned" by the microorganism.

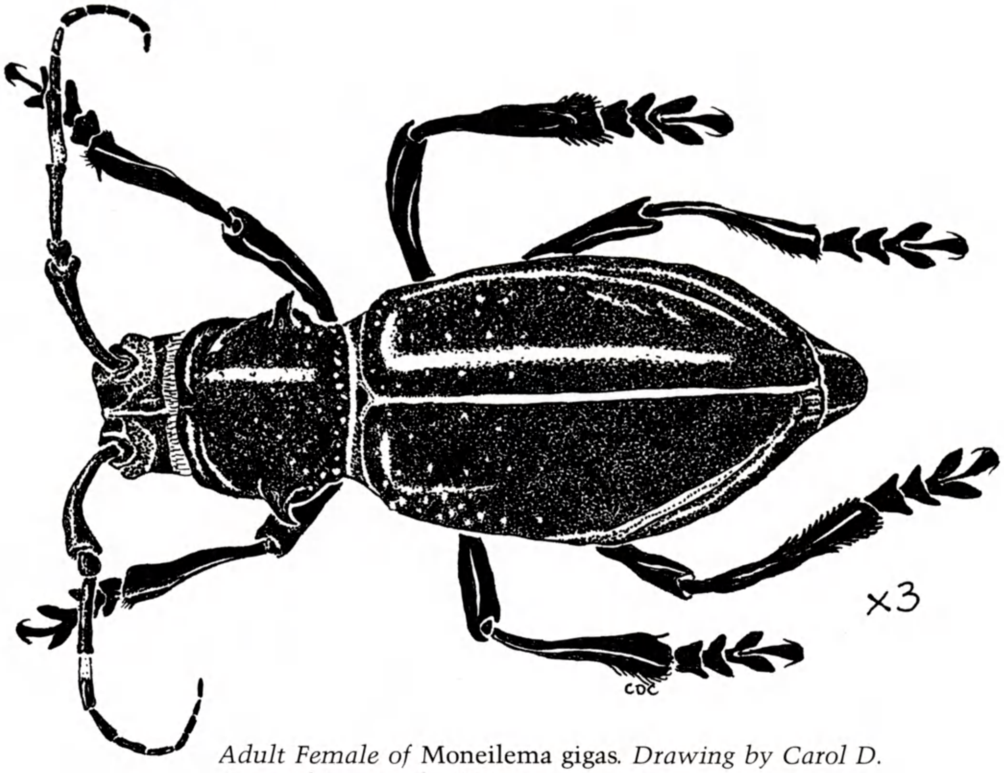
As the food passes through the larval digestive system, microorganisms of the gut come into play to produce the dark-colored frass. The microorganisms of mandibles, gut and frass seem to make a balanced stable flora within the plant and there is not a frank necrosis that might result from a highly pathogenic organism. As larvae mature, pupate and emerge in spring and early summer, however, the succession of microorganisms within the cavities of stems does finally often result in frank necroses which decimate plants and serve as foci for infection which can be spread to other parts by various vectors. Interestingly, this necrosis generally only extends within a *Trichocereus* stem up to a constriction or segmentation of the stem caused when an adult *Moneilema gigas* beetle destroyed the apical meristem. This is thought to be due to the pathogen spreading through soft tissues rather than vascular ones. No soft tissues connect the stem segments. Thus, characteristic damage by a *Moneilema* adult can result in arrest of the necrosis introduced by a *Moneilema* larva.

Destruction of the Vascular System. In every case of larval infestation of *Trichocereus*, we have observed destruction of the greater part of the vascular system, but only up to the end of the stem segment. The destruction seems to result from physical chewing by larval mandibles, apparently in conjunction with the "conditioning" by the weakly pathogenic microorganism. Continued inoculation of the microorganism into new sections of vascular tissue seems to be accomplished by the mandibles. The microorganism apparently does not pass along sections of vascular tissue undamaged by mandibles or it would pass from one stem segment to another, which it does not. After pupation, if the previously infested stem segment has not undergone frank total weeping necrosis (which quickly destroys the entire segment), and if some vascular and surrounding tissues remain intact, adventitious roots may form at the base of the segment. If these grow into the soil, the previously infested segment, although having lost chlorophyll at least below, has been seen to rejuvenate.

Unfavorable Angle of Stem Repose. Even if an infested stem segment completely dies, adventitious roots from the segment above will normally grow down into the old cavity. As the previously infested stem rots away, the adventitious roots from above will contact the soil but the stem will generally fall over rather than remain erect. Even when an infested stem does not entirely die but rejuvenates and forms adventitious roots itself, it often does not remain completely erect. When not vertical, stems of *Trichocereus* become yellowed in Arizona's intense sun of summer, perhaps because they do not properly radiate heat because of the unfavorable angle of stem repose in relation to normal aerodynamics. As a result, old *Trichocereus* plants in Arizona often have unsightly yellowed and crooked bases.

Antifeedants, Alkaloids and Genetic Selection. Among cactus collectors of the world, *Trichocereus* is reputed to have few if any insect or animal pests. We have heard it said that a creature will take one bite of *Trichocereus* and never do it again. We agree that mammals such as packrats, rabbits, or javelinas avoid *Trichocereus*. Both root mealy bugs and spine mealybugs, normally serious pests of cacti, are seldom seen on *Trichocereus*. Many species of *Trichocereus* are known to be rich in alkaloids. Perhaps these may function as antifeedants.

Moneilema, having presumably lived for millenia with both Prickly Pear and Cholla, may well have become genetically adapted to counter certain antifeedants. The fact that *Moneilema* does not overwhelm either the native Prickly Pear or Cholla as it does *Trichocereus* indicates to



Adult Female of Moneilema gigas. *Drawing by Carol D. Crosswhite, April, 1986.*

us that *Opuntia* species likely have become genetically adapted to an equilibrium with the beetle, perhaps by production of additional antifeedants which *Trichocereus* lacks. Also, we must consider the possibility that common races of *Moneilema gigas* of the Arizona desert might not be particularly virulent for *Trichocereus* but that a race adapted to *Trichocereus* chemistry may have arisen. Another possibility is intriguing. Does the microorganism inoculated by the mandibles partially digest the *Trichocereus* tissue so as to denature antifeedants which deter other pests? Is the same microorganism found when *Moneilema* infests *Opuntia*? Is the organism a *Trichocereus* microbe from Argentina which has been transferred to a race of *Moneilema* in Arizona? Our research has not yet answered any of these questions. Interestingly, we find no other species of insects within the *Moneilema* larval cavities of *Trichocereus*. In insect infestations of other cacti, a virtual ecological succession of insects inhabits a single cactus in the same region as our *Trichocereus* study.

Trichocereus as a Complete Host Throughout the Life Cycle of the Beetle. In colonies of *Trichocereus spachianus* which we have studied, *Moneilema gigas* seems to be capable of completing its entire life cycle using this plant and no other. The life cycle begins with mating which occurs on the tops of *Trichocereus* stems. Females deposit eggs at the base of *Trichocereus* and the larvae eventually gain entry to the food stores, mineral nutrients, and moisture of the stem. The larvae make a canal through the frass and exudate of the infested cavity down into the soil at the base of the plant. Here the pupal chamber is made which connects with the canal within the stem.

During winter we find the larva in its pupal chamber at night when the soil is warmer than the stem. In the daytime the larva locomotes through the canal by the friction of its body segments against the frass and plant tissues. By the time of pupation it has systematically eaten a mass of tissue about 60 times its own dimensions and has turned the majority of this into the purulent frass. The pupa remains but a short time in its chamber before metamorphosing into the adult. The adult *Moneilema* is the only insect we know of to chew more than once on a *Trichocereus*. The adult spends a long time eating into the apical meristem and sometimes also into lateral stem areas, obviously being able to digest the tissues. Could the adult have some of the same microorganisms in its gut that seem to "condition" the *Trichocereus* tissues for eating by the larva? If so, perhaps these cope with the antifeedants and are the reason that only *Moneilema* seems to attack *Trichocereus*. Could the lengthy but rather slow feeding at night relate to such a slow digestion process?

Adults re-use the old pupal chamber as a refugium from heat during summer. As a result, we have found them visible only at night or near dawn. Control of the insect on *Trichocereus* is very easily accomplished in summer by picking the adults off of the plants at night with forceps and by removing larvae from yellowed stems in winter. When collected in Kahle's Solution, which keeps them flexible, adults and larvae make excellent teaching specimens because of their large size and classic anatomy.

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