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NOTES ON THE BIOLOGY OF Oncideres bouchardii BATES (Coleoptera: Cerambycidae), A TRUPILLO TWIG GIRDLER FROM SANTA MARTA, COLOMBIA

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RESUMEN

Se describen algunos aspectos de la biología de Oncideres bouchardii BATES de Santa Marta, Colombia. Los adultos de esta especie de escarabajos podadores de ramas, aparecen después de la época de invierno, durante los meses de noviembre a febrero, podando ramas y ramitas de Trupillo, Prosopis juliflora (L.) y Aromo, Acacia farnesiana WILLD. Según las observaciones, la actividad de podar solamente la presentan las hembras, las cuales frecuentemente se encuentran copulando con los machos al mismo tiempo. Después de cortar con sus mandíbulas una estría (ranura profunda alrededor de la rama), la hembra prepara una cámara debajo de la corteza en la cual deposita un huevo. Para ello, perfora la corteza cerca de la base de una ramificación de la rama "anillada" anteriormente, trabajando con una y otra mandíbula. Efectuado esto, se da media vuelta e introduce su ovipositor en el hueco preparado. Por medio de presión de linfa el órgano ahora es inflado y extendido a la vez, forzándose así entre corteza y madera, abriendo la cámara para el huevo. Al parecer la hembra se facilita la localización de la entrada a esta cámara por medio de una marca que aplica sobre la corteza con su ovipositor, mientras que esté preparando la entrada a la cámara con sus mandíbulas. Cada huevo es depositado en una cámara particular, la cual es sellada después con una sustancia que se endurece al entrar en contacto con el aire. Después de aproximadamente una semana nace la larva y empieza pronto a enterrarse en la madera de la rama. Esta suele secarse y caer del árbol a causa de la estría, la cual impide el flujo de la savia. El ciclo de vida de Oncideres bouchardii dura un año, ocupando su mayor parte el estado larval. Los adultos viven menos de una o dos semanas, en pocos casos solamente se observó que algunos llegaron a vivir hasta 45 días.

En localidades donde las destrucciones en los árboles ya llegaron a ser muy notorias, se recomienda la recolección y quema de las ramas y ramitas "anilladas", controlando así huevos y larvas que puedan vivir en ellas.

SUMMARY

Aspects of the biology of Oncideres bouchardii Bates from Santa Marta, Colombia are described. Imagines of this twig girdler appear shortly after the rainy season

during the months of November to February, ringing twigs and branches of trupillo trees, Prosopis juliflora (L.) and aromo bushes, Acacia farnesiana WILLD. Observations showed that this activity is only performed by the females, which commonly copulate at the same time. After girdling the twig, the females lay their white eggs one by one into especially prepared egg cavities that are sealed after oviposition.

There is evidence that locating the entrance to the future egg chamber with the ovipositor is greatly facilitated by means of a marking on the bark made with the ovipositor while making the entrance with the mandibles. The eggs are deposited by means of the telescopic and inflatable ovipositor which is inserted deeply under the bark through hemolymph pressure and acts to force open the egg chamber between bark and wood. After approximately a week the larvae hatch and soon dig into the drying twig.

The lifecycle of Oncideres bouchardii lasts one year, the longest part of it belonging to the larval stage. Most imagines live less than a week or two, although a few survive as long as 45 days.

In places where much destruction of the trees is caused by this twig girdler, it is recommended to collect and burn the girdled twigs or branches that contain the woodboring larvae or eggs of the species.

INTRODUCTION

Most longhorned beetles (Cerambycidae) tend to oviposit into dead wood. Some go a step further and kill the wood for their larvae. Such a behaviour is demonstrated by Oncideres bouchardii that severs twigs or stems from living trupillo trees, Prosopis juliflora (L.) and aromo bushes, Acacia farnesiana WILLD., both Mimosaceae.

It was found that almost all trupillos on the desert-like hillsides surrounding Santa Marta have twigs and stems that seem to have been cut off by means of a sharp tool (Fig. 1). The ground beneath the trees is covered with the dry severed branches that range in diameter from about 0.5 to 3.0 cm. The cut stumps have blunt, conical ends.

Cerambycid larvae were found within the cut branches in August 1976, but the search for adult beetles was without success from March through most of December of the same year. Finally, in late December, fresh girdling on some branches announced the renewed activities of the beetles (Fig. 2). Inmediate search yielded several pairs in copula and some single individuals of the species Oncideres bouchardii (Lamiinae: Onciderini), that may be called the trupillo girdler.

GIRDLING

Succeeding observations showed that the twigs are girdled by the females of these beetles. Soon after dark the sexes meet, copulate and the females start girdling a suitable twig or branch, usually still in copula (Fig. 3). Two obvious conditions for the selection of twigs are their thickness and their being alive. The position of these twigs or stems within the tree may vary greatly, from the very center to more peripheral areas.

Clinging to the part of the branch that will eventually fall off, she moves around it slowly, gnawing with her mandibles, and now and then throwing away pieces of bark and wood by foreward and lateral movements of her head. In this way a groove is cut around the twig. During the beginning of the cut the female maintains her first pair of legs on

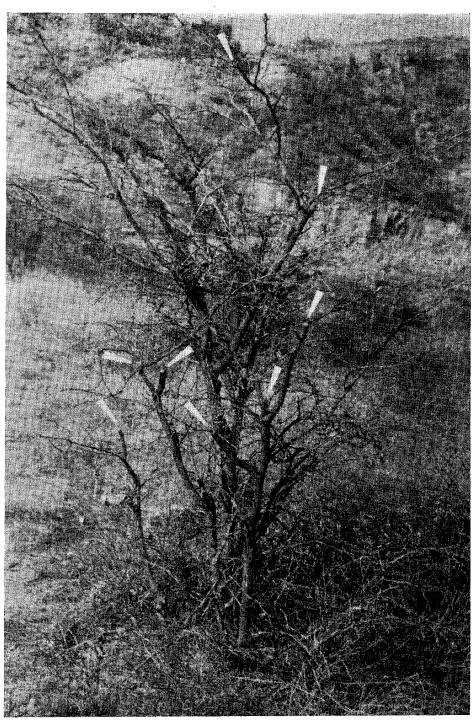


Figure 1. Characteristic aspect of a trupillo, *Prosopis juliflora* (L.), that has partly been destroyed by the twig girdler *Oncideres bouchardii* Bates. Some sixty twigs and branches have been severed in the course of the years, leaving a seriously affected tree that merely reaches human height. Arrows indicate some of the stumps.



Figure 2. Through girdling the sap flow is stopped, the twig dries and finally dies off, falling to the ground or staying entangled in the branches.

one rim of the notch, the second pair being placed on the other side of it. Later on, after the notch is deeper, she keeps her first pair of legs within the notch. Possibly by this means, the direction and width of the cut is assessed, thus helping to form the almost perfectly circular groove (Figs. 2 and 3).

The depths of these notches, however, are rather variable. One can find relatively shallow cuts that just reach through the bark layer and also deep grooves that leave only a narrow central connection. In any case, the flow of the sap is interrupted, and sooner or later the branch dries and falls off. To girdle a twig as thick as a finger, the female gnaws from one-half up to three quarters of an hour; thicker branches require correspondingly more time. In some cases finishing the groove took the female two consecutive nights. In a few instances, exceptionally heavy sap flow prevented prolonged girdling, thus saving the branch. One may speculate that in this manner, the trees have the ability to defend themselves from being totally destroyed by the trupillo girdlers. After the notch is finished, the pairs most often remain copulating through the night until the next morning.

FEEDING

During the morning hours the individuals separate and wander independently through the branches, feeding on the bark of young sprouts and shoots. This feeding produces characteristic irregular scars where the outer bark layer has been scraped off. Sometimes the areas fed upon become so extensive that the affected branches eventually die.

OVIPOSITION

After feeding, the female prepares to lay her eggs. With her head being directed towards the distal end of the branch, she perforates the bark at the bases of side branches of the previously girdled stem or twig, gnawing and digging with her mandibles alternatively. When the left mandible is being used to perforate, the right is anchored in the bark to the side of the hole for support. When the right mandible digs, the left is anchored to the other side (Fig. 4). Thus, the female leaves a scar at each side of the entrance to the future egg chamber (Fig. 5). While

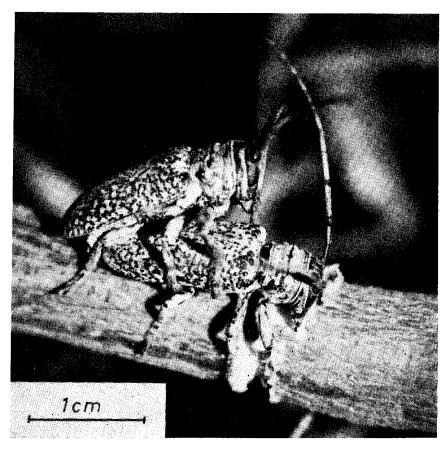


Figure 3. The twigs are girdled by the females that commonly copulate at the same time. The photograph shows the almost perfect circular groove just before completion.

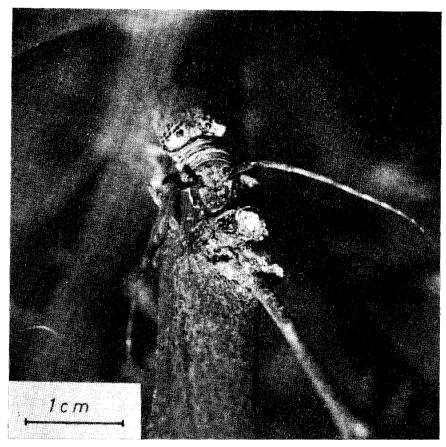


Figure 4. At the bases of sprouts and small side branches the female cuts a hole through the bark layer through which it will insert its ovipositor.

engaged in perforating, the female from time to time touches the surface of the bark with the tip of her abdomen and the slightly protruding ovipositor (Fig. 6). When the perforation is complete, she turns 180° until her mouthparts are directly over the spot previously touched by her ovipositor. It seems likely that some substance is deposited by the ovipositor that helps the female subsequently match the ovipositor to the entrance hole by simply matching up her mandibles to where the ovipsitor formerly was. Then, with a few wagging movements of her abdomen, the ovipositor again being partly extended and feeling its way, the female locates the entrance and introduces the ovipositor (Fig. 7). Now, by hemolymph pressure, she extends this organ even more and forces it between the bark layer and the wood in the same direction that she faces. Closer observation reveals that the slight inclination of the entrance hole and the likewise oblique position of the ovipositor when inserted into the hole, provide the necessary leverage for the now expanding ovipositor to lift the bark. The end of the extended ovipositor is then fully inflated, opening a cavity into the cambium layer (Fig. 8).

A single white egg is then deposited into this cavity (Fig. 9), probably after having deflated the ovipositor. In order to retract the balloon-

like organ back into her body, the female uses a special device. Within her abdomen we find a long, chitinous shaft, one end of which proyects deeply into the body cavity, the other being connected ventrally to the base of the ovipositor. Muscles originate on the free end of this shaft and insert within the ovipositor. When the latter is fully extended, these stretch equally. When the organ is to be retracted, the muscles contract and, being fastened to the inner parts of the ovipositor, thereby draw this organ back again into its telescoped position within the female's body.

On withdrawing her ovipositor, the female seals the entrance to the egg cavity with a drop of a brownish liquid (produced by accessory glands?) that hardens in contact with air (Figs. 5 and 9). The time needed for perforation of the entrance hole, forming of the egg chamber, oviposition and finally sealing of the entrance is less than five minutes. Chambers that contain an egg are readily identified by their seal at the entrance and also by a slight swelling of the bark just proximal to it. Unsealed entrances indicate empty chambers.

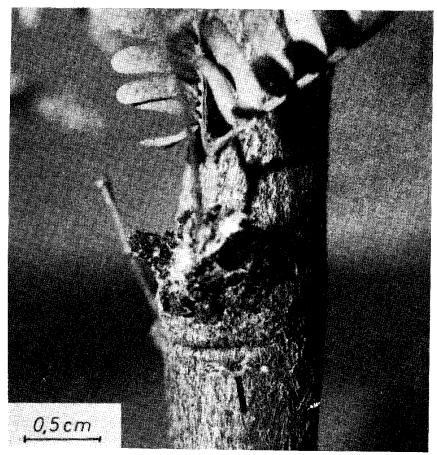


Figure 5. After oviposition the entrance to the egg cavity is sealed by a shiny secretion that hardens in contact with air. To the sides of the entrance two punctures can be seen that were made alternately by the anchored, non-digging mandibles. The line indicates the egg chamber seal.

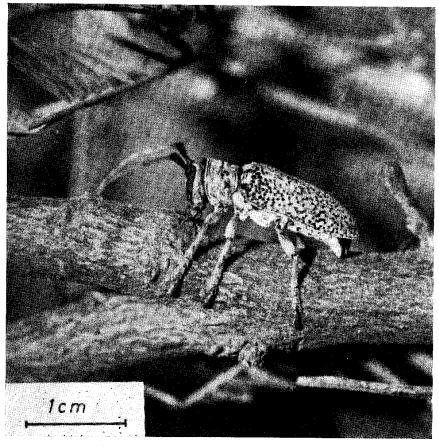


Figure 6. During the preparation of the entrance to the future egg chamber, the female occasionally touches the bark with the tip of her abdomen. At this time the ovipositor is extended slightly to touch and thereby mark the spot.

LARVAE

After approximately a week, the larvae hatch. As no empty egg shells are found in egg chambers in which larvae have hatched, it seems reasonably clear that the larvae feed on their shells after eclosure and then start digging into the plant tissues. After some three to four weeks, they expell frass from the now opened entrance to their egg cavity, thus revealing their activity. Most often at this time the drying twig is still fastened to the tree, held by the central connection that was left. Depending on its thickness and the depth of the groove, the branch slowly dries, finally breaking off and falling to the ground or remaining entangled within the branches. Comparing twigs that had fallen with twigs that had stayed in the trees it was clearly seen that twigs hanging in the branches contained a considerably higher number of Oncideres larvae than the ones that had fallen to the ground. Thus it seems likely that there is an advantage to the larvae whose host-twig stays within the tree. This may be due in part to the fact that ground and undergrowth are populated by several predatory ant species, whereas in the trees we normally find but one species, Camponotus lindigi MAYR which attends two honeydew producers: coccids and the riodinid caterpillar Hamearis erostratus Westw.

These ants apparently do not harm the developing beetles. They moreover seem to keep other ants away from the trees. However, microclimatic differences between canopy and soil, and/or parasites may also cause differential survival in the two sites.

TERRITORIALITY

Female trupillo girdlers are strongly territorial towards other females. This was most clearly seen when another female was placed experimentally next to a cutting female. Instantly she stopped gnawing, localized her competitor and seemingly with much exitement started to bite and push the intruding female until the latter fell from the branch. Having accomplished this, the female went on searching all over "her" branch for further intruders and did not resume her work for a long while.

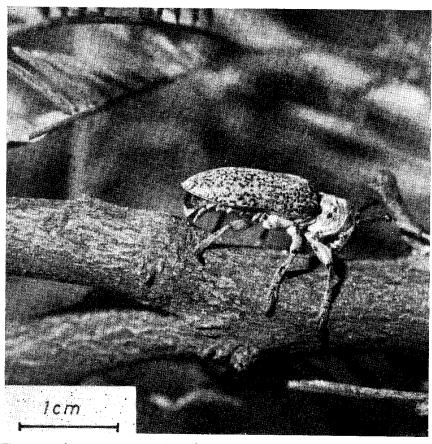


Figure 7. After turning around 180°, the female locates the previously marked point on the bark with the palps of her mouthparts. It seems evident that by this means the problem of finding the entrance hole is much facilitated. In the photograph the ovipositor is being introduced into the hole.

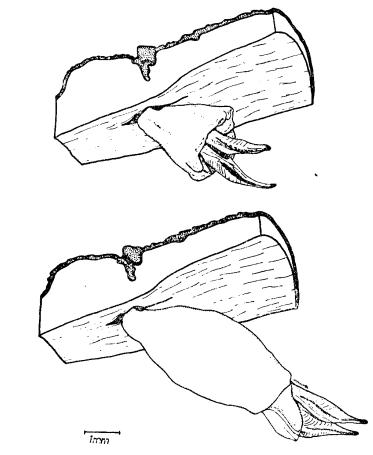


Figure 8. A piece of bark removed from a twig, showing the ovipositor projecting underneath: a) semi-inflated; b) fully expanded. The ovipositor was cut from the beetle while ovipositing.

LONGEVITY

In the second year of this study (1977), in a small area next to the Instituto de Investigaciones Marinas de Punta de Betin in Santa Marta, 29 individuals on five trupillo trees were marked on their elytra with nail polish. With the exception of the weekends, almost daily checks and counts of these marked individuals were made at noon. The results in Table 1 show that most beetles lived less than a week or two, although a few managed to survive as long as 45 days.

That year the trupillo girdler season started in the first half of November, probably due to the early beginning of the dry season, and ended with the disappearance of the remaining five marked individuals on December 30th of the same year. These were the last of both marked and unmarked beetles in the study area. In a more humid region (Nenguangue Bay) to the northeast of Santa Marta, several individuals were collected a few days later, but from then on, no more Oncideres bouchardii were seen.

Table 1. Longevity of Oncideres bouchardii according to sightings of 29 marked individuals. Only 5 beetles lived as long as 45 days.

Number of individuals:	12	5	2	2	2	1	1	5
No. of days sighted on trees:	1	5	6	7	9	11	14	45

Table 2. Observed combinations of copulating individuals. Below each female are listed in order the males with whom she copulated. Note that female No. 23 chose male No. 20 twice, and that some males mated with several females.

φ:	10	11	13	17	18	21	23	25
	5	15	12	16	19	20	22	24
♂:	15	20		24			20	
				26			29	
				29			20	

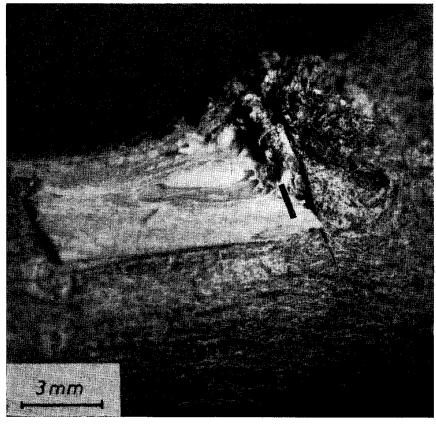


Figure 9. The elongated white egg is inserted into the somewhat larger cavity made by the balloonlike end of the ovipositor. The line indicates the egg chamber seal.

LIFECYCLE AND FERTILITY

From Table 2 it can be seen that females will commonly copulate several times, up to four were observed. They may do so twice with the same male on different occasions. Knowing that after each copulation a new twig is selected, and that in each of them we may find up to 24 eggs, one can calculate a reproductive potential of at least 96 eggs per female per season. In view of the complicated procedure accompanying oviposition, and the probability that even more unobserved copulations took place, this is an astonishing feat.

The lifecycle of *Oncideres bouchardii* lasts one year, the longest part of it belonging to the larval stage. Imagines were found from December 1976 to February 1977 and from November 1977 to January 1978. They eclose, then mate, and the females start laying eggs at the beginning of the dry season, depending on when the rains have provided fresh twigs and branches.

DISTRIBUTION AND HABITAT

Based on the few samples of this species collected since its description by Bates in 1865, the distribution of *Oncideres bouchardii* is northern South America. Individuals have been taken from Santa Marta, Colombia (Type locality: Santa Martha, New Grenada), Caracas, Venezuela and Santarem, Brazil (from Dillon & Dillon, 1946). Personal observations in the region of Santa Marta, and reports by reliable people of the trupillo girdler's damage throughout the arid Guajira Peninsula in northeastern Colombia, suggest that the species prefers a dry habitat and xerophytic vegetation.

DISCUSSION

The present observations show that girdling in Oncideres bouchardii is a strictly female activity, commonly performed when copulating.

Working with Oncideres rhodosticta on mesquite (Prosopis glandulosa Torr.) in Texas, United States of America, Polk and Ueckert (1973) found also that only females were involved in girdling.

This, however, differs markedly from what REUTER (1913) tells us about Oncideres impluviatus girdling a Melastoma sp.: "male and female worked together in the preparation of the groove, shifting from place to place deepening the notch until the stem fell off" (transl. by present author). A drawing is added that shows both beetles side by side at work on the upright stem. Since the text indicates that REUTER did not get his information firsthand, and since this behaviour is rather fundamentally different from other Oncideres species so far known to me, his account may be a misinterpretation of an original source that said simply "the two sexes worked together", but meaning in copula. Though his account may very well be true, it should be reconfirmed.

POLK and UECKERT found females of O. rhodosticta girdling during the day. This was never seen in O. bouchardii. During the day males and females rest motionless on twigs and branches, some may feed and oviposit at dawn and/or dusk, but cutting begins only after sunset. Ano-

ther behavioural difference between O. bouchardii and O. rhodosticta is in the distinct position of their heads when preparing the entrance to the future egg cavity. O. rhodosticta faces towards the base of the tree (POLK and UECKERT), while O. bouchardii faces in the opposite direction (Figs. 4 and 6). This difference can be explained by the fact that not all Oncideres species will deposit their eggs at the bases of buds and side branches as O. bouchardii mostly does.

HIGH (1915), studying Oncideres putator on the huisache tree (Acacia farnesiana) in southwestern United States, found that this species may lay her eggs anywhere along the branch girdled and does not so particularly about buds or at the bases of small branches. The same appears to be true for O. rhodosticta. These species can therefore puncture the bark while in different position, whereas for O. bouchardii the only "practical" position to do so seems to be facing towards the distal end of the cut twig.

The time needed for the females to lay an egg varies from species to species. The procedure is very similar in all three girdlers, but the time needed for the preparation of the egg cavity until sealing the chamber entrance is 20 to 30 minutes in O. rhodosticta, about 15 minutes in O. butator and less than 5 minutes in O. bouchardii. No reasonable explanation for the latter's exceptionally rapid oviposition can be given. Nevertheless, as escape during this time is impossible, a short oviposition appears advantageous in order to avoid predators.

A study on the oviposition of a european long-horned beetle, Saperda populnea (L.) revealed that after having deposited her egg in a cavity under the bark of popular or willow trees, the female sealed the entrance hole with a gelatinous substance. In addition to sealing the entrance, and thus protecting egg and larva from predators, this substance breaks down plant tissues surrounding the egg (from Jacobs & Renner, 1974). Whether this is true in the case of the seal of the three species of Oncideres here mentioned remains to be investigated.

CONTROL

According to observations on Oncideres rhodosticta infesting mesquite trees (Prosopis glandulosa) in a study area in the Trans-Pecos region of Texas, United States of America, about 90% of the trees had been attacked by the beettles and about 40% of all limbs from 0.5 to 2.0 cm in diameter had been girdled (UECKERT, POLK and WARD, 1971; POLK and UECKERT, 1973). HIGH (1915) observed as many as 63 girdled branches, the work of Oncideres putator, in one huisache tree (Acacia farnesiana) in southwestern United States.

From the present study, it can safely be said that the destructions inflicted by the trupillo girdler to the trupillo trees, Prosopis juliflora, and to a lesser extent to the aromo bushes, Acacia farnesiana (= huisache tree), in the Santa Marta region, about equalize the damage caused by the huisache girdler (O. putator) and the mesquite girdler (O. rhodosticta) in their respective regions of the United States of America.

Nearly all parts of the beetle's favoured trupillo have ecological and economical value. Next to several cacti and thorny underwoods, trupillo and aromo are among the few plants that provide ground cover on the dry mountain slopes near Santa Marta. During the short but heavy rainfalls that once or twice a year tear deep ravines in the ground, their tough roots help to keep the soil from being washed away. Consequently these trees are important for conservation of the soil and thus its poor flora. According to Pérez-Arbeláez (1956), the fruits of the trupillo are eaten by men and beasts. The bark of these trees is also being used as thatching material for houses in the Guajira Peninsula. Their wood is much sought after because of its resistance to seawater. Stems and thicker branches are used to make beams and ribs for the seafaring canoes.

In some places, the evidence of the beetle's presence is quiet impossible to overlook. No tree may be left without the typical stumps of severed twigs and stems, and the floor underneath them strewn with dried branches. In such cases it would seem advantageous to stop further destruction. This could be achieved most effectively by burning the dried branches, as was already suggested by High (1915) for the control of the huisache girdler. With the exception of the months of November to February, during which the imagines could escape by flying away, every time in the year is suitable for such an action. In this way all eggs and wood boring larvae could be destroyed, thus keeping the trees healthy.

ACKNOWLEDGEMENTS

I am indebted to Prof. Dr. F. Schremmer, Heidelberg, Germany and to Mr. T. J. Spilman, U. S. Department of Agriculture, Washington, USA, who have provided literature and helpful comments. Dr. C. Kugler, Santa Marta, Colombia, kindly assisted with the preparation of the english text. My wife, Heide, made the drawings.

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