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THE BIOLOGY OF *PANCHLORA NIVEA*, WITH OBSERVATIONS ON THE EGGS OF OTHER BLATTARIA

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Biology of *Panchlora nivea*

Little is known of the biology of the pale-green Cuban cockroach, *Panchlora nivea* (Linnaeus). Various biological observations on purportedly different species of *Panchlora* may refer to *P. nivea*. Rehn and Hebard (1927) listed seven names that have been used for West Indian species of *Panchlora*. These workers stated: "There is a strong possibility that in most cases they relate to *P. cubensis*, the dominant West Indian species, but their arbitrary reference to that species would hardly be warranted." Gurney (1955) has shown that *P. cubensis* Saussure is a synonym of *P. nivea* (Linnaeus). Hebard (1917) stated that Shelford, after examining the types, placed *P. virescens* in synonymy under *P. nivea*. Rehn and Hebard (1927) stated that without more explicit information on the type, *P. viridis* (Fabricius) must be considered to be an unidentifiable species of the genus. However, Hebard (1917) identified as *P. cubensis* (= *P. nivea*) many of the adventives that had been reported by others as *P. viridis*. Where the synonymy is evident, we have discussed the species as *P. nivea;* where it is not, we have retained the name assigned by the original observer.

Panchlora nivea is the dominant species of the genus in the Greater Antilles, and it is widely distributed in Mexico, Central America, and northern South America; it is the one most frequently encountered adventive in the eastern United States, being regularly transported to this country in bananas (Rehn and Hebard, 1927). According to Hebard (1917) *P. nivea* is found established in the United States only in the vicinity of Brownsville, Texas; it is essentially an out-of-doors tropical form that can not adapt itself to artificial surroundings, and which, he stated, can never become established north of the tropical areas of this country.

In Puerto Rico, *P. nivea* is found in the rotting trunks of palm or coconut trees where it feeds on the rotting brown fibers in which it tunnels (Seín, 1923; Wolcott, 1950). The nymphs are brown and resemble those of *Pycnoscelus;* they require 100 days to mature; the female produces 30 nymphs per oötheca (Seín, 1923). Scudder (1890) reported that *P. nivea* is viviparous and this was confirmed by Riley (1890, 1891). Riley reported that a female of this species gave birth to about 30 young. He dissected another female and found a semicircular-shaped oötheca containing about 44 eggs. The oötheca consisted of a thin membranous sheath which covered the basal half of the egg mass. Riley believed that hatching occurred in the genital pouch within the abdomen of the female and that this pouch was so large that the young could move about and undergo " postnatal development ". Hansen (1894) found a museum specimen of a female *P. " viridis "* which had an egg capsule protruding from the end of her abdomen. Bayford (1934) claimed to have observed *P. " viridis "* (or *P. exoleta* Burm.) giving birth to about 30 young, and stated that no oötheca was extruded, nor could he find one after dissecting the female. Davis (1930) stated that a female *P. nivea* kept in captivity gave birth to about 20 young without producing an egg capsule. He reared two males to maturity; one took a little over 6 months to mature, the other nearly 8 months. Shelford (1906) observed a live specimen of *P. nivea* which had an oötheca partially protruding from the end of her abdomen; the oötheca was " complete " as compared to the " incomplete " membrane in the specimen observed by Riley. Shelford concluded that in his specimen the egg mass was so large that it could not be retained entirely within the brood sac. Chopard (1938), probably taking his information from Riley and Shelford, stated that the oöthecal membrane of *P. " viridis "* and *P. nivea* is incompletely formed and tends to disappear.

The oöthecal membrane of *P. nivea* when first laid down covers nearly all of the eggs. It is possible that Riley's observation, that the membrane envelops no more than half of the eggs, was based on an oötheca in which the embryos were well developed; in this case the increase in the size of the developing eggs may have decreased the area covered by the oötheca. Actually, the

oötheca is so thin and practically colorless (except for light amber colored edges) that it is difficult to see the extent of the membrane (Plate XXII, fig. 9) unless the eggs and oötheca are separated (Plate XXII, fig. 10). Although Bayford (1934) claimed that no oötheca was extruded by *P. " viridis "* at parturition, it is possible that he observed the young shortly after they were born by which time they may have eaten the oötheca and embryonic membranes, a common practice among " ovoviviparous " cockroaches.

We have established a colony of *Panchlora nivea* from a single female collected by Edna Roth, May 12, 1956, on bananas in a store in Framingham, Massachusetts. After 26 days in the laboratory, kept at 24° C. and 50 to 60 per cent R. H., this cockroach gave birth to 60 young. Nineteen days after giving birth, the female was observed with an oötheca protruding beyond her wing tips; within 55 minutes she had completely retracted the oötheca into her brood sac. Sixty days after oötheca formation this female gave birth again. She died October 12, 1956, after having lived 153 days in the laboratory; she fed on banana skins and Purina Dog Chow checkers. At autopsy we found a J-shaped oötheca, containing 53 eggs, in the brood sac. The oötheca was tightly enveloped by the uterus which filled most of the body cavity.

The ovipositional behavior of *Panchlora nivea* is similar to that found in species of *Gromphadorhina, Pycnoscelus, Nauphoeta, Leucophaea,* and *Blaberus* (Roth and Willis, 1954). The female *Panchlora* that Shelford (1906) reported as carrying an exposed oötheca was either in the act of ovipositing or had prematurely extruded the egg case. Premature extrusion of the oötheca by cockroaches that incubate their eggs in a brood sac may occur when they are killed (Roth and Willis, 1954); this probably explains Hansen's (1894) observation (see above).

Contrary to Riley's opinion the nymphs, during normal birth, do not move about in the genital pouch after the eggs hatch. We have observed birth once in *P. nivea,* and the act of parturition in this species is no different from that in species of *Leucophaea, Nauphoeta,* etc.; the oötheca containing fully developed eggs is re-extruded, and once the embryos are clear of the confines of the

female's body they free themselves completely from their enveloping membranes and drop from the oötheca. Apparently under abnormal conditions it is possible for an embryo to hatch within the brood sac. When one of our females died, she partly extruded her oötheca. None of the exposed embryos were able to free themselves from the enveloping membranes and oötheca. On dissecting this female we found that the oötheca had broken into two parts; the anterior part, containing ten embryos, remained tightly invested by the anterior end of the brood sac. One embryo had shed its embryonic skin almost completely; only its tarsi were still encased. This nymph had already become tanned, and it is conceivable that at a later stage of development it might have shed its skin completely and moved about in its cramped quarters. This abortive hatching was possible because the broken oötheca, having separated, left an empty space in the brood sac which was prevented from collapsing by the eggs that distended the anterior and posterior parts of the uterus. An empty brood sac contracts to a fraction of its distended size.

Twenty-three nymphs from the first litter of 60 were reared to maturity. Males (N = 10) [1] matured in an average of 144 ± 8.0 [1] days and females (N = 13) in 181 ± 6.3 days. The mean number of nymphs per litter from 14 births was 46.1 ± 2.4 (range = 28 to 60). The mean time to the birth of the first litter for seven females isolated after mating was 55.3 ± 1.8 days (range = 50 to 62 days). If we allow about a week after mating for oviposition to occur, then embryogenesis takes an average of about 48 days at 24° C.; it will be recalled, however, that the first female used to establish the *P. nivea* colony, gave birth 60 days after oöthecal formation. Three of the seven females gave birth again 63.3 ± 2.9 days after the first birth. One female gave birth to a third litter.

We have observed the mating behavior of *P. nivea* several times. When confronted with six-day-old virgin females, males that are several days old simply run rapidly around behind the female, back up to her (Plate XXII, figs. 1, 2), and quickly make connection. The final mating position, during which time the

[1] N = number of individuals from which mean values were computed. The figures at the right of ± are standard errors.

spermatophore is transferred, is end to end with the heads of both individuals facing in opposite directions (Plate XXII, fig. 3). The average time spent in copulo was 40 ± 2.4 minutes (range = 30 to 46 minutes, N = 7). Six-day-old females mated readily; the males mated with these without any apparent preliminary courtship. The female does not feed on a secretion on the male's tergum nor does she assume the superior position prior to copula, as has been reported for several other species (Roth and Willis, 1954). Females four and five days old did not mate as readily as those six days old. With these younger females, the male behaved differently. He moved around the female slowly and stopped near the end of her abdomen where he rocked from side to side and at the same time arched his abdomen downwards so that his wings were held slightly away from his body. He then slowly backed up toward the end of the female's abdomen and remained quiescent in this position for some time. The younger female may actively resist the male's attentions by kicking with her hind legs or by running away.

The precopulatory position in *Panchlora*, in which the male simply backs up to the female and makes connection, differs from that known for all other cockroaches in which mating has been observed. Although Ramme (1923) stated that the male of *Ectobius* backed up to the female, this was questioned by us (1957) and found not to be true in *Ectobius pallidus*. Rau (1922) made a single field observation on the mating of *Parcoblatta pensylvanica* (DeGeer) and claimed that the female was the aggressor and attempted to back under the male (this would be a male superior pose). This precopulatory position is highly doubtful. We have observed the courtship of *Parcoblatta virginica* (Brunner); this species behaves like other species of cockroaches in which the males have a tergal gland. The male of *P. virginica*, after touching the female with his antennae, raises his wings to about a 45° angle; he may remain in this position for a time if the female that he is courting does not respond. If the female begins to feed on his tergal secretion, he raises his wings to 90°, and when her mouthparts reach his first abdominal segment, he pushes backwards and grasps her genitalia. The pair then assume a position, typical of blattids, with their heads facing in

opposite directions. Males of *P. virginica* are attracted to courting males and feed on the male tergal secretion just as the females; this feeding stimulates the courting male to attempt copulation.

In practically all species of cockroaches, the female is above the male just prior to genital connection. The only exceptions so far as we know, are *Panchlora nivea* and *Pycnoscelus surinamensis* (Linnaeus).[2] In this latter species we did not observe any courtship by the male; he simply climbed onto the back of the female and twisted his abdomen down and under that of the female (Plate XXII, figs. 4-6); connection was readily made from this male superior pose, somewhat like the behavior of grasshoppers. After connection has been made, the final mating position (Plate XXII, figs. 7, 8) is similar to that of other cockroaches. The mean time spent in copulo by *Pycnoscelus* was 23 ± 1.2 minutes (range = 15 to 26 minutes, N = 8), during which time the spermatophore was transferred to the female.

Water Relations of the Eggs of Some Blattaria

Recently (1955) we discussed the water uptake by cockroach eggs and showed that the initial water content of eggs and oöthecae of species that incubate their eggs in a brood sac is considerably lower than the water content of the oöthecae and contained eggs of oviparous species. Table 1 gives the percentage of water not previously reported in the newly formed oöthecae and eggs of seven species of cockroaches. The relationship of a relatively low initial water content in the eggs and oöthecae of false ovoviviparous cockroaches in comparison with the oviparous forms (except *Ectobius pallidus*) is again borne out. Table 2 shows the changes with age in water and dry matter content of eggs of *Panchlora nivea* and two species of blaberine cockroaches which also incubate their eggs in a brood sac. The water content of the eggs of these species increased with age but there was no corresponding increase in dry matter which is so characteristic of embryonic development in *Diploptera punctata* (Roth and Willis, 1955a).

[2] *Pycnoscelus surinamensis* is parthenogenetic in the United States and apparently no males occur in nature in this country. We obtained three males which were reared from nymphs that were accidentally included in a shipment of *Diploptera punctata* (Eschscholtz) from Hawaii. A bisexual colony of *Pycnoscelus* has been established in our laboratory.

TABLE 1. Water content of newly formed oöthecae and their enclosed eggs from several species of cockroaches

Species and type of oviposition behavior	Water content (%) ± S. E.[1] of oöthecae and eggs	N[2]
Oviparous species which deposit and abandon the oötheca shortly after its formation:		
(1) *Ectobius pallidus* (Olivier)	40.0 ± 0.61	5
(2) *Neostylopyga rhombifolia* (Stoll)	64.3 ± 0.61	5
(3) *Parcoblatta virginica* (Brunner)	56.9 ± 0.68	5
(4) *Periplaneta brunnea* Burmeister	64.5 ± 0.43	5
False ovoviviparous species which extrude then retract the oötheca and carry it internally until the eggs complete development:		
(1) *Blaberus craniifer* Burmeister	36.0	1
(2) *Byrsotria fumigata* (Guérin)	34.7 ± 0.56	3
(3) *Panchlora nivea* (Linnaeus)	37.0	1

[1] S. E. = standard error
[2] N = number of oöthecae

Ectobius pallidus overwinters in the egg which seems to undergo diapause. Sometime before hatching, the eggs pick up water which causes the oötheca to swell (Roth and Willis, 1957). Nothing is known about the rate of uptake of water by the eggs of this species. On April 16, 1957, some overwintering oöthecae and a few nymphs (older than first instar) of *E. pallidus* were collected in Plymouth, Massachusetts. These oöthecae had not yet begun to swell visibly. The water content of five of these oöthecae was 41.0 ± 1.1 per cent. We had previously determined that the water content of newly formed oöthecae of this species (deposited in the laboratory) was about 40 per cent (Table 1). Thus the eggs of *Ectobius pallidus* apparently do not pick up water during the winter months since the water content of the eggs collected in the field in April (and which had been deposited in the previous summer or fall) was essentially the same as that of newly formed oöthecae.

The oöthecae were divided into two groups; one group was kept continuously on filter paper moistened with distilled water; the second group was removed from moist paper after nine days. The uptake of water is shown in text-figure 1A. Both groups of oöthecae rapidly increased in weight for four days; those eggs kept moist continuously (text-fig. 1A, solid line) then slowly increased in weight from the fourth to the twenty-first day at which

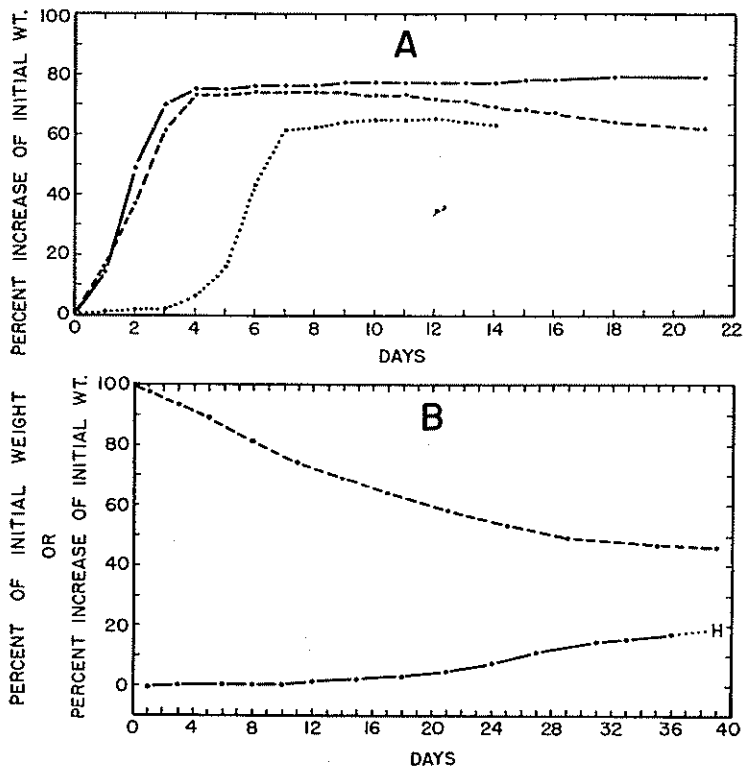
TABLE 2. Changes in wet weight, water, and dry matter of eggs of three species of false ovoviviparous cockroaches

Note: The actual ages of the eggs, except for the newly or recently formed oöthecae, were unknown. The eggs are arranged in order of increasing wet weight which, being correlated with development, represents an increase in age. The weight of the oötheca is included in the computations. All values were determined from one oötheca for each wet weight listed.

Species	Milligrams Per Egg		
	Wet weight	Dry Matter	Water
Blaberus cranüfer	13.2 [1]	8.4	4.8
	19.8	7.6	12.2
	25.4	7.1	18.3
	25.6	7.4	18.2
	30.0 [2]	8.2	21.8
Byrsotria fumigata	13.1 [1]	8.6	4.5
	15.3 [1]	9.8	5.5
	16.0 [1]	10.6	5.4
	27.4	8.8	18.6
	27.9	9.8	18.1
	28.4	7.8	20.6
	29.4	9.4	20.0
Panchlora nivea	0.4 [1]	0.3	0.1
	0.7	0.2	0.5
	0.8	0.2	0.6
	1.0 [2]	0.3	0.7

[1] Newly or recently formed oöthecae.
[2] Well-developed embryos.

time the eggs began to hatch. It is estimated from known dry weights of oöthecae that at the time of hatching the oöthecae and eggs of group one contained about 75 per cent water. The second group of oöthecae (text-fig. 1A, broken line) similarly increased in weight until the ninth day. After the ninth day the eggs were placed on dry filter paper and they began to lose water gradually. However, in spite of this water loss the eggs in these oöthecae hatched on the twenty-second and twenty-third days. It is apparent that if sufficient moisture is absorbed, the eggs may subsequently lose some water, when subjected to dry conditions, but still complete development and hatch.



Text-figure 1.—A. Uptake of water by eggs of *Ectobius pallidus*. The oöthecae had overwintered in the field and were taken into the laboratory on 16 April, 1957. The axis of abscissas represents the days after the oöthecae were first placed on filter paper moistened with distilled water. The plotted points are mean values.
.——.= Six oöthecae kept on moistened paper until the eggs began to hatch on the twenty-first day.
.– – –.= Five oöthecae kept on moistened paper for nine days and then kept on dry filter paper.
. . . . .= One oötheca kept on moistened filter paper for fourteen days; see text.

B. Oöthecae of *Parcoblatta virginica* deposited in the laboratory. The axis of abscissas represents the age of the oöthecae. The plotted points are mean values.
.——. = Five oöthecae kept on moistened filter paper; the change in weight is expressed as the per cent increase of the initial weight. The last weighing was made on the thirty-sixth day and the eggs hatched (H) on the thirty-ninth day.
.– – –. = Ten oöthecae kept on dry filter paper at 50 to 60 per cent relative humidity. The loss in weight is expressed as a percentage of the initial weight. None of the eggs hatched.

A single oötheca behaved somewhat differently from the others; its weight changes are plotted separately (text-fig. 1A, dotted line). This oötheca showed very little increase in weight for the first three days on moist filter paper, but after the third day it began to pick up water more rapidly. Apparently at the time this oötheca was collected, the eggs had not reached the stage in development when they begin to absorb water through the oötheca. By the fourth day water began to be absorbed, and the subsequent weight curve is similar to the others described previously. After the twelfth day on moist paper, this oötheca began to lose weight, so it was dissected on the fourteenth day; many of the eggs were well developed having dark eye spots, but some embryos apparently had died and therefore had begun to lose weight.

In the field, the eggs of *Parcoblatta virginica* are deposited in relatively moist situations, under logs, bark, etc. In the laboratory, the female usually deposits her oöthecae on the moist cotton stoppers of vials containing drinking water. Those eggs not deposited on the moist cotton do not develop at room humidities and the oöthecae frequently collapse. This is similar to the behavior of the eggs of *Cariblatta lutea minima* Hebard.

The initial water content of oöthecae and eggs of *P. virginica* is about 57 per cent (Table 1). After two weeks, when kept on moist filter paper, the eggs begin to absorb water through the oötheca and continue to do so at a slow uniform rate, as represented by weight gain (text-fig. 1B, solid line), until hatching occurs on the thirty-ninth day. It is estimated that at the time of hatching the oöthecae and eggs contained about 67 per cent water. If the eggs are kept on dry filter paper at 50 to 60 per cent R. H., water is lost steadily, as represented by weight loss (text-fig. 1B, broken line), and the eggs fail to develop.

The oöthecae of *P. virginica* differ from those of some other oviparous species (e.g., *Blatta orientalis, Periplaneta americana*) in apparently not possessing an impermeable coating which retards loss of water from oöthecae that are exposed to relatively dry conditions. The eggs of *P. virginica* do not undergo diapause; in this respect they apparently differ from the eggs of *Ectobius pallidus*.

Summary

Panchlora nivea extrudes its oötheca during formation and then retracts it into a brood sac where the eggs develop. When the embryos mature, the oötheca is re-extruded; the nymphs free themselves from their enveloping membranes, as the oötheca is forced from the brood sac, and drop from the female. One mating enabled a female to produce three litters. The mean number of nymphs per litter was 46. Embryogenesis took about 48 days at 24° C. Male nymphs matured in an average of 144 days and females in 181 days. The mating behavior of *P. nivea* differs from that which has been observed in other cockroaches in that the male backs up to the female to make genital connection, and the female does not feed on any secretion on the male's tergum. Another peculiar mating behavior among the Blattaria is that of *Pycnoscelus surinamensis*, the male of which makes connection with the female after climbing on her back. The final mating position of both *Panchlora* and *Pycnoscelus* is similar to that of other cockroaches; the sexes, with genitalia joined, face in opposite directions.

The water contents of oöthecae and eggs, not previously reported for several species of cockroaches are given. The eggs of *Panchlora nivea, Blaberus craniifer*, and *Byrsotria fumigata* increase in water content, but not dry matter, during embryogenesis. The eggs of *Ectobius pallidus* overwinter in the field with essentially no change in water content. Oöthecae of *E. pallidus* that had overwintered in nature were brought into the laboratory and kept moistened; they absorbed water rapidly for four days and then increased in weight slowly until the twenty-first

day when the eggs hatched. The oöthecae of *Parcoblatta virginica* are deposited in moist situations. In the laboratory, eggs of *P. virginica* that were kept moist began to absorb water after two weeks and increased in weight slowly until hatching on the thirty-ninth day. When the oöthecae of *P. virginica* were kept at 50 to 60 per cent relative humidity, the eggs lost water steadily and did not hatch.

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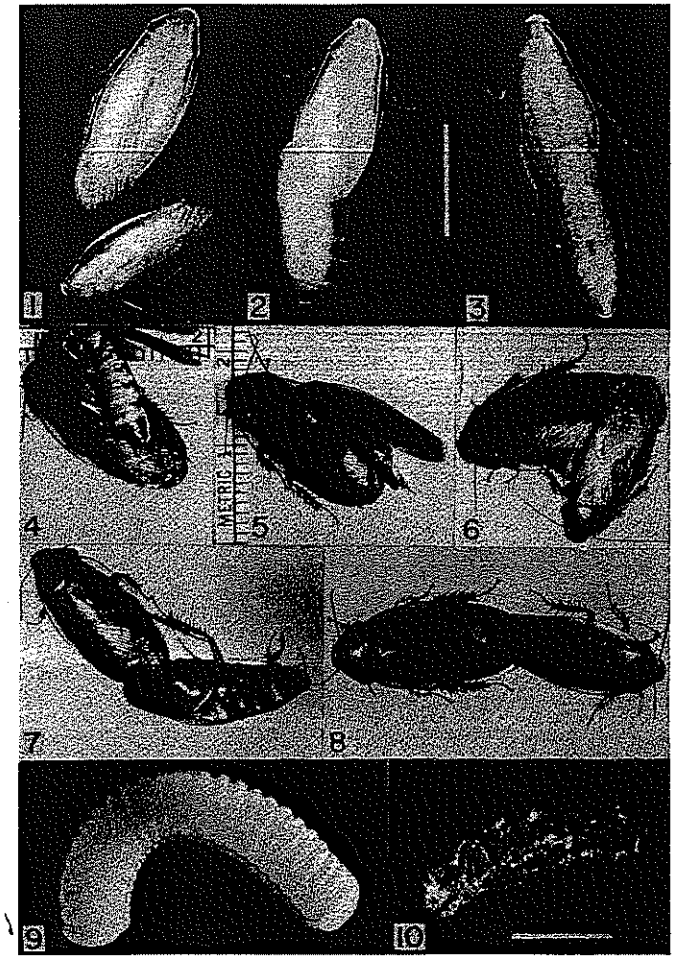
Explanation of Figures

PLATE XXII

Figs. 1-3.—*Panchlora nivea*. 1. Male moving around to posterior end of female. 2. Male (blurred) backing into female and making connection. 3. Pair in copulo. Vertical bar = 1 cm.

Figs. 4-8.—*Pycnoscelus surinamensis*. 4-6. Male on female attempting to make connection. 7. Pair connected, with male twisting around to assume an upright position. 8. Final mating position.

Figs. 9-10.—*Panchlora nivea*. 9. Oötheca and eggs removed from female. 10. Thin oöthecal membrane separated from the enclosed eggs. Horizontal bar = 3 mm.



ROTH AND WILLIS: PANCHLORA NIVEA