Life history of Alagoasa bicolor (L.) in indoor rearing conditions[1])

(Coleoptera – Chrysomelidae – Alticinae)

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Abstract

Alagoasa bicolor (L.) (Alticinae) was successfully reared on its hostplant in outdoor and indoor conditions. Mating, and development from eggs to adults was followed in petri dish cultures. Timing of the stages in these conditions was approximately as follows:

Eggs	10 days
Larva I	8 days
Larva II	7 days
Larva III	11 days
Prepupa	2 days
Pupa	10 days
Subterranean adult	2 days
TOTAL	50 days

The female oviposits on the soil. Larvae spend most of their time in lethargic aggregations on the soil. The pigmentation of prothoracic and anal shields of the larvae serves as a criterion of the instar: in the first instar they are black, in the second, gray, and in the third, they approximate the general body color. A prominent exuvium of oesophageal chitine is drawn out at the larval moltings. This might be a genus specialty, because in *Omophoita,* an anal exuvium was seen to be more prominent.

Introduction

Blake (1927) preliminarily published Böving and Craighead's (1931) illustration of a larva of *Omophoita gibbitarsa* Say, providing at the same time data on host plants, oviposition, and pupation. Later Nevermann (1933) made the surprising claim that larvae of Oedionychina are intestinal parasites of man(!). So far as we know, this exhausts the information published on the life history of Oedionychina. The Australian C.S.I.R.O. scientists in Brazil have successfully reared 2 to 3 *Oedionychus (Alagoasa)* spp. for weed control purposes (Winder 1976), but details have not been published.

[1]) Dedicated to Jan (deceased) and Bohumila Bechyné.

This modern subtribe of fleabeetles possesses unusual cytological characteristics (Smith and Virkki 1978, Virkki 1983), which could be better studied if one of the species could be safely reared in the laboratory. We have therefore tried to rear the two more common Puerto Rican species, *Omophoita cyanipennis* F. and *Alagoasa bicolor* (L.). In our primitive rearing conditions, we have not overcome a high larval mortality in the former species, but we trust that *A. bicolor* can now be reared outdoors and indoors, on its hostplant. The following is an account on the life history of *Alagoasa bicolor,* as it appears from our laboratory cultures.

1. Material and methods

From June, 1979 to April, 1980, *Alagoasa bicolor* was collected weekly from the vigorous, *Aegiphila martinicensis*-associated deme of Vega Alta, where the specimens are larger than in other consulted *bicolor* sites (Virkki 1982, Virkki and Zambrana 1980). The species is breeding all the year around (Virkki and 1979 a). Pairs in copula were isolated in glass tubes and used for establishing cultures. Other copulating pairs were later obtained from the main sample wiped from the *Aegiphila* bushes and kept in plastic bags in the laboratory.

Two kinds of cultures were established:

1.1. Rearing in plexiglass cages of 76×60×31.5 cm, provided with two round, covered openings for the hands. The 76×31.5 cm floor of the cage was divided by plexiglass partitions into 6 compartments 18 cm high and of equal size. These compartments were filled with the soil (Almirante clay) from Vega Alta, and *Aegiphila martinicensis* cuttings were planted in each. The watering was through plastic tubing of 2.5 mm inner diameter, connecting each of the compartments with a 500 ml plastic water receptor placed on the top of the cage. Draining was through holes in the bottom.

The cages were kept in two places: 1) in a well ventilated greenhouse at the Agricultural Experiment Station in Río Piedras, near sea level; and 2) outdoors in half-shade at Carraízo Alto (elevation 160 m above sea level). No breeding was possible at Carraízo Alto, but in Río Piedras, a self-perpetuating stock could be maintained.

An even infestation of *Aegiphila martinicensis* in nature suggests that injure-based chemical defense systems (Haukioja and Niemel 1977, Carroll and Hoffman 1980) do not operate against *A. bicolor* in this plant (but the other hostplant, *Clerodendron aculeatum,* being unevenly infested, might well have them: Virkki 1980). Indeed, it is sufficient to rear in outdoor cages on *Aegiphila,* if there is a simple need to produce all developmental stages for experimentation. But if more intimate morphological or behavioral studies of the preadult stages are conducted, then smaller, transparent vessels that can be placed under a microscope, become necessary. Thus we reared a fraction of the material in petri dishes, just to learn to know the stages of metamorphosis.

1.2. Rearing in 9 cm ∅ petri dishes. The bottom of the dishes was covered by a soil layer of about 0.7 cm thick. Several such dishes wrapped in newspapers were autoclaved at

175°C and stored for use. One pair of *A. bicolor* found in copula was placed in each of the dishes, together with a piece of *Aegiphila martinicensis* leaf. The piece of the leaf was substituted daily by a new one. If eggs were laid, the parents were transferred to a new dish, to avoid damaging the eggs.

The dishes, provided with the date of establishment of the culture, were kept on a desk illuminated during 12 h daily by four tubiform Lifeline Sylvania 110/40 W bulbs located 241 cm right above the desk top. The relative humidity was about 70%, the average temperature 25.4°C (8.00 h) and 27.7°C (17.00 h). Most observations on the normal course of life history were made under these conditions.

We reared also in non-autoclaved petri dishes with natural soil, but infestation of the egges by fungi and mites increased significantly. Materials like "Kimwipe" paper and fragments of termite nests were tried as alternative oviposition surfaces, but they were inferior to soil.

For illustration, we used an awkward but well-working device: an old Ihagee Exacta camera mounted on a Bausch & Lomb stereo-zoom microscope. Shades were neutralized with a white paper cylinder, illuminated from opposite directions by two Bausch & Lomb Nicholas illuminators.

2. Results and Discussion

2.1 Wild adults in culture

2.1.1 Survival

The life of a couple in petri dishes was observed until one of the beetles died. In 40 cultures, the survival varied from one to 121 days, the average being 23.4 days. Possible reasons for a short survival are an advanced age and unnoticed damage at collecting. Different pathological conditions could of course develop in the rather limited, closed space of a petri dish under our semi-sterile conditions. Larger rearing boxes as other entomologists (Schaber et al. 1975, Furth 1982) have used, might have saved more lives.

A rough ocular estimation of the leaf area eaten by a couple was made daily. The amount varied from 0.01 cm^2 to 1.45 cm^2, the average being 0.59 cm^2/day/couple.

2.1.2 Copulation

In order to assure an attraction between the sexes, we established cultures only with pairs found in copula.

In copulation, the male mounts the back of the female. During a few seconds, at intervals that may last from minutes to hours, the male strokes the antennae and the anterior part of the body of the female with his antennae. The female may or may not respond in a similar way. The copulating pair stays usually at the same spot if not disturbed. But the female may walk and even eat during copulation. Separation occurs without ceremony, although we have seen once how the male made a few rather vigorous side-to-side movements just before separation. Such a behavior during copulation is somewhat different from the Alticinae standards (Furth 1982).

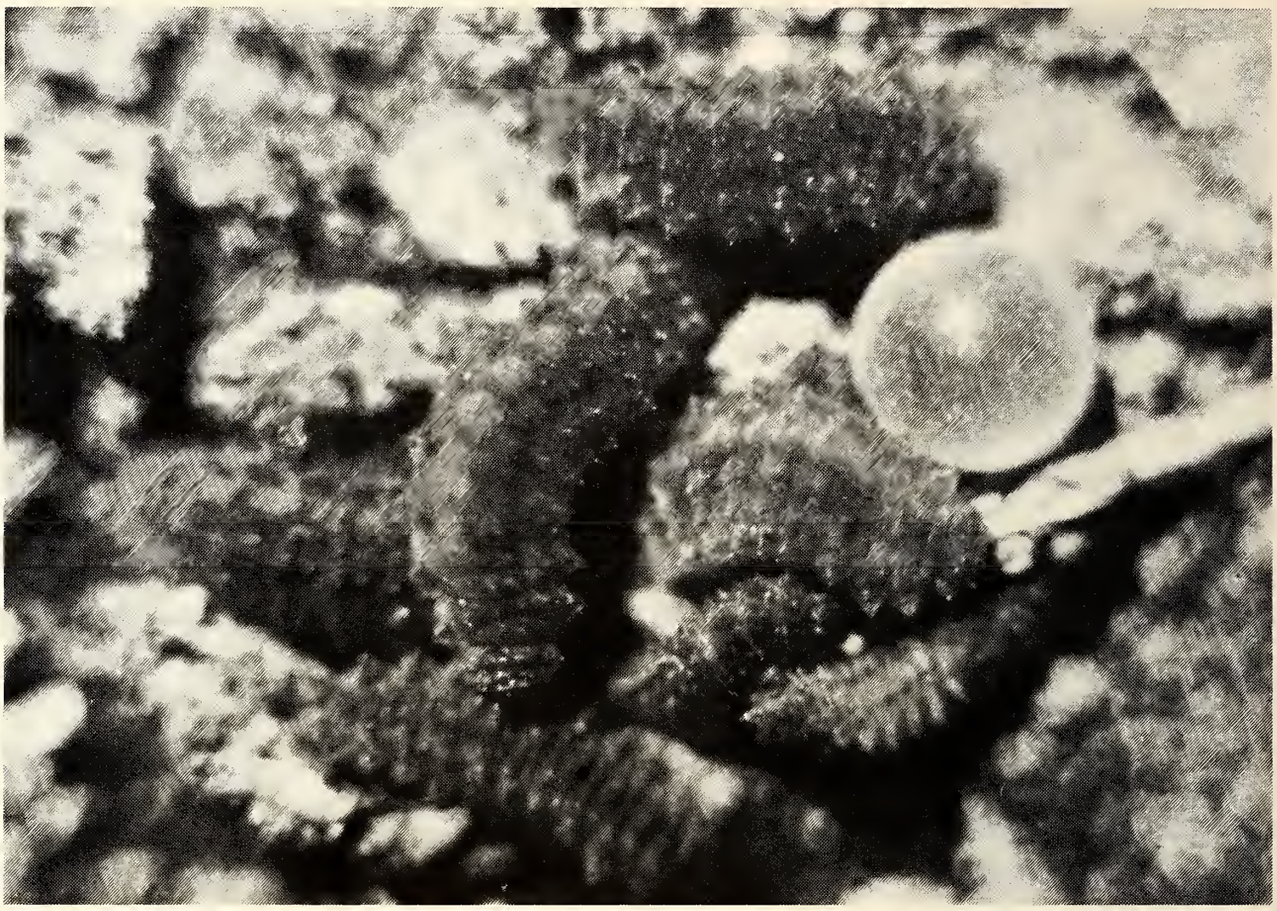

Fig. 1. *Alagoasa bicolor*. Seven of eight sister larvae (see p. 139) of the third instar aggregated on the ground. – Diameter of the plastic pearl: 5 mm.

Duration of the copulation is very variable. We have recorded cases from a few seconds to over 14 hours, the average for 70 copulations lasting over 1 h being 4.8 h. As we seldom observed both the initiation and the end of a copulation, the actual time must be notably longer. A copulation which starts late in the afternoon may last overnight. Such a long time might be necessary for transportation, and accomodation in the female, of the extra long sperm cells that leave the male as coiled bundles (Bruck 1978).

The frequency of copulation. Copulation was observed in practically all cultures established. It can occur at any time between ovipositions, even immediately after one. Excluding intervals shorter than one day, the observed intervals between copulations varied from one to 20 days, the average being 4 days. In a culture kept for 99 days, 11 copulations were observed, in another lasting 120 days, 24 copulations took place. As many copulations must have escaped our observation, all frequencies mentioned are too low. In nature, under normal living conditions and with more than one male per mature female available, the frequencies might be notably higher.

Initiation of the copulation in young animals. Because the recently born beetles remain for a couple of days hidden in their pupal cells, we do not have much data on the age when the sexual attraction begins. In three couples we had to abandon for a "force ma-

jeur", no copulation occurred during the first 10 days of fully pigmented, freely moving adults. In one of these pairs, both beetles were young; in the other two, only one was young. In another case, a female copulated at the age of 10 days with a wild male, and a young male at the age of 24 days with a wild female. Once initiated, copulations occurred at a normal frequency in these two pairs.

2.1.3 Oviposition

A. bicolor has two ovaries, each one containing about 10 ovarioles. Eggs mature simultaneously in all ovarioles (Virkki 1979 b). Thus a female is expected to lay about 20 eggs at intervals determined by the duration of maturation of the ovarial eggs.

The expectancy was not met by the females of our cultures, which produced only an average of 13.7 eggs per cluster. Autopsy of four females deceased in the culture revealed $9_4 10$, $8_4 8$, $8_4 8$, and $7_4 8$ ovarioles per individual. It is possible that the well-established deme of Vega Alta has an ovariolar number reduced from the average determined by Virkki (1979 b) from a Salinas deme occupying a more problematical niche (Virkki 1980). On the other hand, a failure of several ovarioles in egg production is a factual possibility, because one female was found to lay the following series of eggs in her successive ovipositions: 17, 9, 19, 13, 2.

A gravid female disturbed by too crowded or otherwise unnatural conditions may lay all eggs scattered on diverse surfaces. A relaxed female in conditions imitating the natural ones (soil and host plant present) lays her eggs in one cluster on the soil (Fig. 2). Natural crevices of the soil are preferred and often haphazardly improved by the female before laying the cluster. Exposed as well as leaf-covered areas of the soil surface have been accepted for oviposition. This pattern of oviposition is common for most fleabeetles (Steinhausen 1981). Contrary to our observations, Blake (1927) reported cases where *Oedionychus* spp. laid eggs on the hostplant in a scattered fashion.

Both clustered and solitary eggs stand erect, fixed to the surface by their distal (non-micropylar) ends. The micropylar end shows a rounded depression. Recently laid

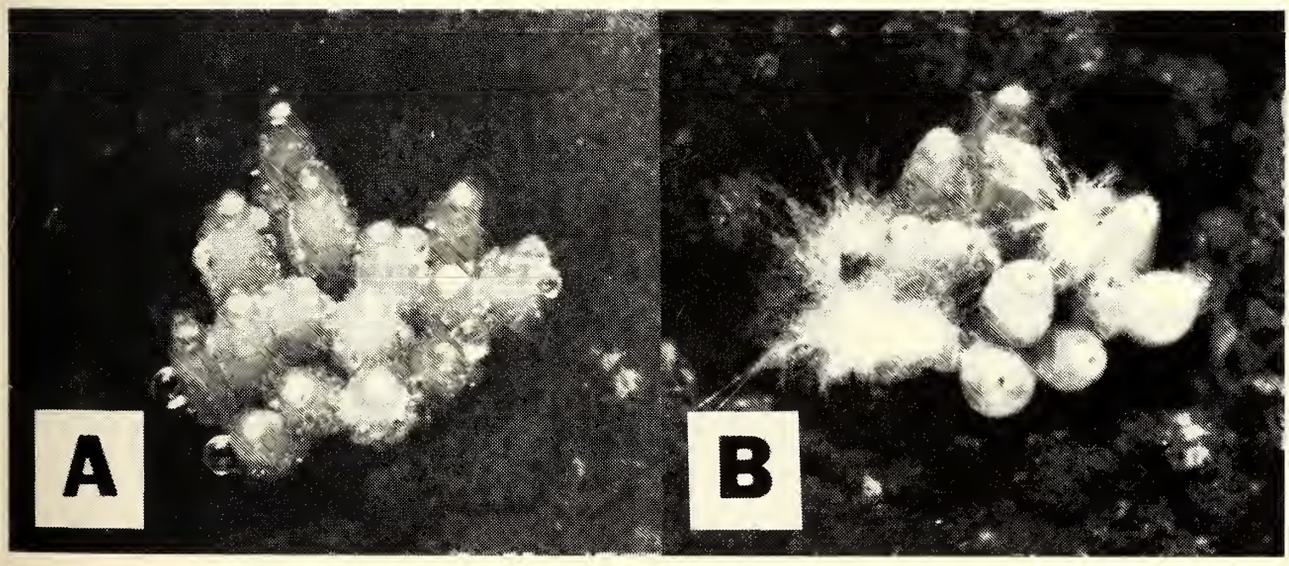

Fig. 2 A and B. Egg clusters of *A. bicolor*. – A. Cluster of 15 recently laid eggs in high humidity. – B. An older cluster attacked by fungus. – Magnification 15×.

Fig. 3. An egg cluster destroyed by mites (two large ones pointed by arrows). – Magnification 26×.

eggs are pale yellow. In higher relative humidities, they are covered by clear droplets, of which the topmost is usually the largest (Fig. 2 A). Within a couple of days, the eggs darken to brownish yellow. The eggs are about 2.5 mm long.

The intervals between ovipositions performed by the same female varied much. We made 13 reliable observations concerning this. The interval was either about 1 week (7, 7, 8, 9, 9 days), 3 weeks (22, 23, 26 days), 5 weeks (34, 35, 36, 39 days), or, in one case, 13 weeks (90 days). We do not know the significance of this discontinuity. It was not due to individual differences.

2.2 Progeny

2.2.1 Egg development

We have only five reliable records on the duration of the egg stage: 10 (3 cases), 9, and 11 days; thus 10 days is the average. Whole clusters, or single eggs, often flatten and produce no larvae. Presumably, such eggs have remained unfertilized, despite the repeated copulation of the parents. Other hazards the eggs have to face in the cultures are:

2.2.1.1 Cannibalism. The parents are capable of destroying the eggs biting them, and although they probably never eat them, the larvae do eat them. As soon as an oviposition has taken place, the parents must be transferred to another dish. Similarly, larvae must be isolated from the eggs.

2.2.1.2 Fungi (Fig. 2 B) were the most serious killers of eggs in our cultures, especially at the beginning, when we tried to keep the soil moistened by occasionally dropping distilled water on it. Eggs that become heavily infested by fungi in the first week do not survi-

Fig. 4. Recently ecloded, incompletely pigmented larvae. Moderate fungus infestation of the eggs. Obs. the shape of the eclosion cut in the eggs. – Magnification 15×.

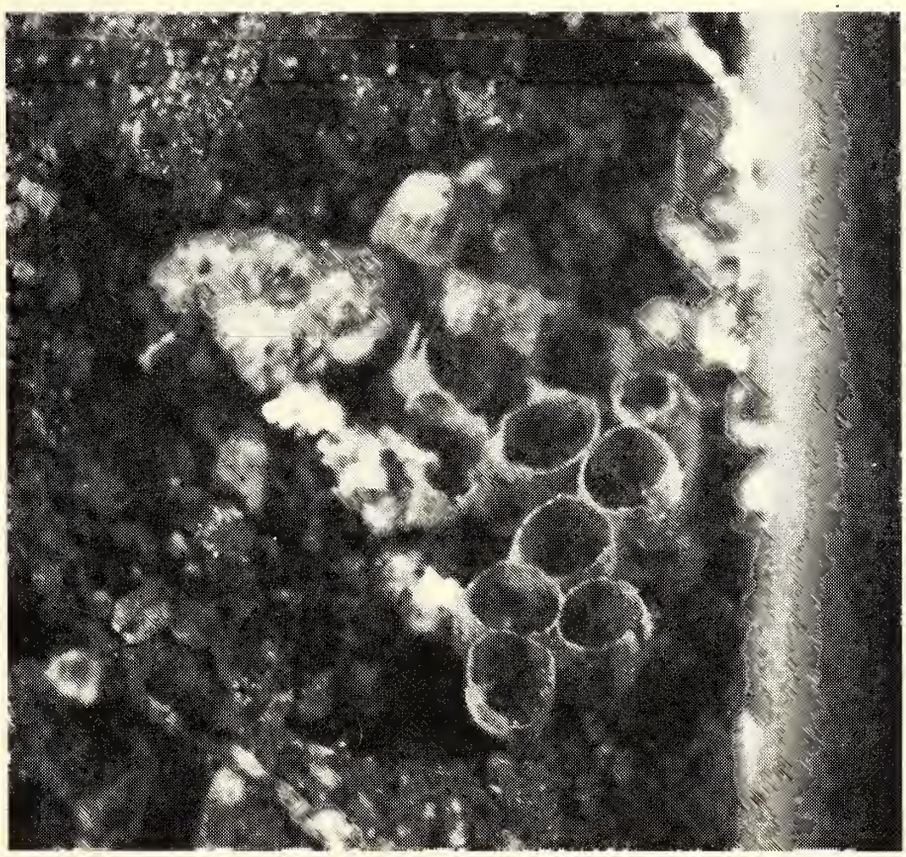

Fig. 5. Egg shells partly eaten by the larvae after eclosion. – Magnification 15×.

ve. Treatment of moderately infested eggs with 0.01% propionic acid may help to save them. The best remedy is, however, to keep the soil dry (the air humidity being 70%). In comparison, eggs of *Omophoita cyanipennis*, a species of more humid natural sites (Virkki 1980, 1982), are more resistant to fungi, and can be bred on a moderately moist soil (Virkki 1981).

2.2.1.3 Mites (Fig. 3) destroy physically damaged eggs rapidly, but attack also healthy eggs. Because we occasionally encountered mites in our semi-sterilized cultures, we suspect that they can enter either on the bodies of the parents, in the foodplant leaves, or walking out from a soilbag kept nearby and entering the closed petri dishes. Mites can be a real nuisance in cultures where the soil is not autoclaved.

Embryogenesis was not studied in detail. Mitoses occur in embryos of all ages. Flores (1982) prefers eggs of four days for colchicine-arrested mitoses, even though at least

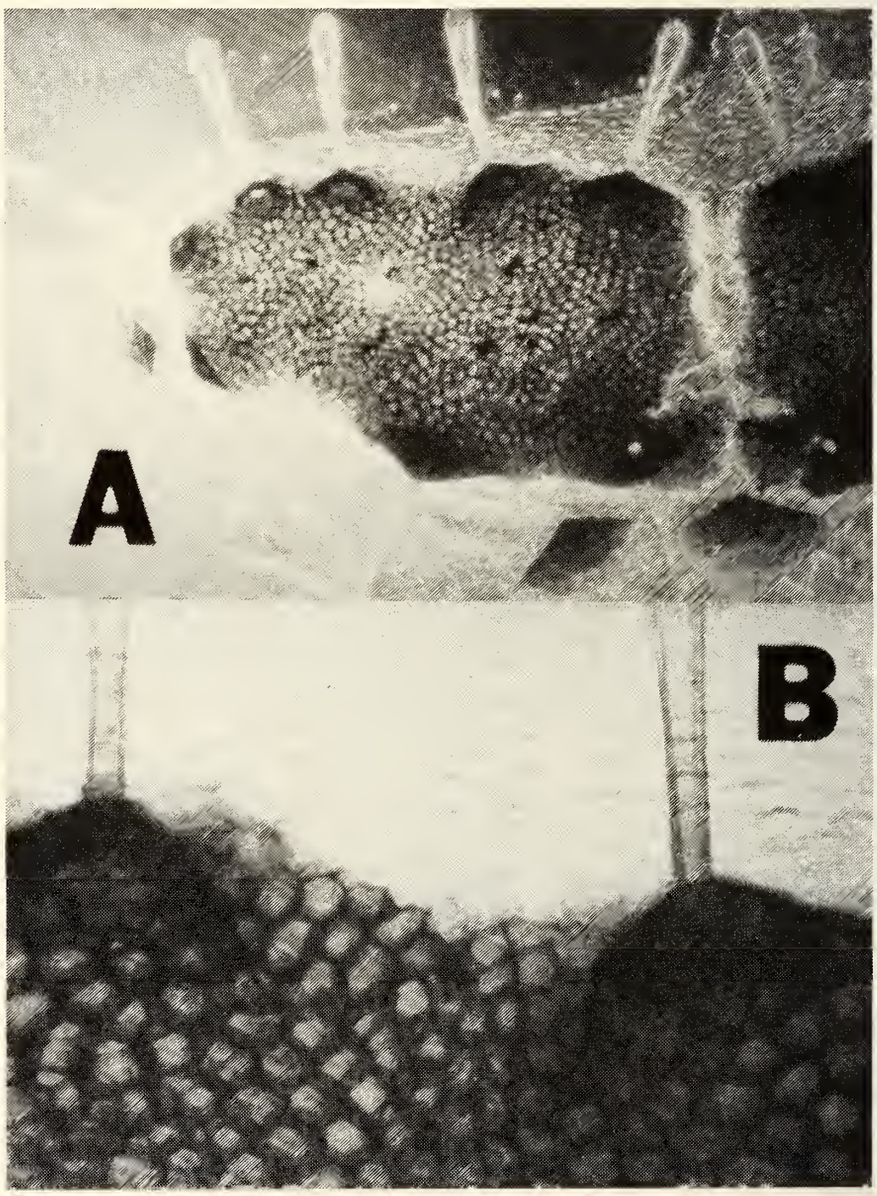

Fig. 6 A and B. Prothoracic shield. – A. Left half of the shield of a fullgrown first instar larva. Fore edge has 5, hind edge 3 protuberances, each one provided with a club-shaped bristle. – B. Enlargement of a part of A. The cell walls of the shield are pigmented and thickened. – Magnifications: A 97×, B 400×.

two cell categories are dividing then. Younger eggs tend to have excessive amounts of yellow oil which disturbs the view in provisory phase contrast observations.

2.2.2 Eclosion of larvae

A larva matured in the egg cuts the egg wall starting with an arc near the top, and continuing vertically down until about $^2/_3$ of the egg length has been cut open. The operation leaves a smoothly triangular lap which yields when the larva forces its way out to liberty (Fig. 4). This mode of eclosion differs from the one described for *Altica* (Woods 1918). Often, but not always, the empty egg shells are partly consumed by the larvae (Fig. 5). In the first two hours, the larvae are pale, with four dorsally located black spots characteristic of fleabeetle larvae (Woods 1918). Pigmentation proceeds rapidly.

2.2.3 The first instar larvae

A young larva is about 3 mm long (4 to 5 mm when walking). The shining black head capsule is about 0.7 mm in breadh. Two retractable antennae are short and transparent. Dorsally, in the segment behind the head, there is a "yoke" formed by two thickened, black, rough-surfaced plates. A black upper surface covers also the ninth body segment. These are the prothoracic and anal shields (Woods 1918). These black surfaces distinguish a first instar larva from the later instars. Magnification of these surfaces shows thickened and deeply colored cell walls (Fig. 6). Bristles of the major body protuberances are club-formed (Figs. 6, 7). The main body color is orange to red, the points of the segmental

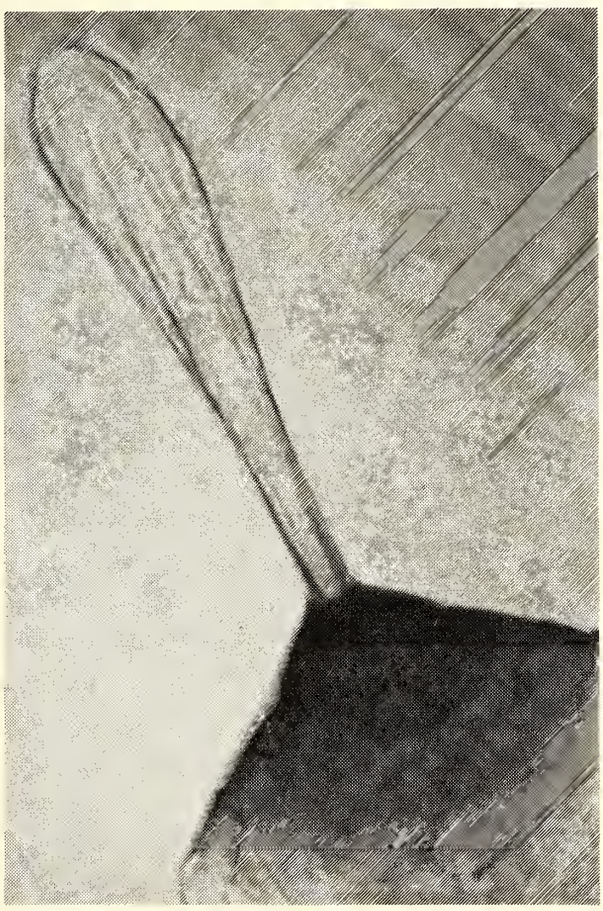

Fig. 7. A dorso-lateral protuberance with a typical, apically swollen bristle. – Magnification 400×.

protuberances being the darkest. There are four dorsal and two lateral lines of protuberances, each provided with a transparent bristle. We give this description only to show how inadequate it is to hold these creatures for "intestinal parasites". A closer description of these and some other Oedionychina larvae has been left to Dr. Walter R. Steinhausen, Austria.

The larvae are moderately light shy, and tend to hide soon if theirbirth site is well illuminated. After having tasted the egg shells, the larvae fast for the following 1 to 2 days. The following case history shows typical activities of the first instar larva:

30. VI. 79	9.00:	7 larvae 1 day old
	18.00:	One larva tries to eat, biting unsuccesfully the edge of a leaf; does not swallow anything, if not a little juice
1. VII.	14.10:	One larva eating a little, tasting both young and older leaves
2. VII.	9.00:	Eating well. Three larvae remain small, other grow rapidly
3.– 4. VII.	:	Four large larvae found aggregated, hidden, immobile on the ground; their skin looks oily, brilliant
5. VII.	18.30:	Molting starts.

As a rule, feeding was concentrated to 1–2 days, thereafter a sluggish aggregation and hiding phase followed. Larvae lagging behind in growth are common, and seldom capable of passing through moltings. The larvae do not need drinking water. Fully grown first instar larvae measured about 7 mm in length. Duration of the first instar was reliably observed in 7 cases: 5, 6, 7, 8, 10, 10, and 11 days, averaging 8.1 days.

In four cases, consumption of *Aegiphila* leaves was estimated ocularly during the instar, and found to be 0.032, 0.029, 0.023, and 0.006 cm^2 per day per larva. The larvae of the last sample survived only three days after the first molting.

2.2.4 First molting

The above case history continues 5. VII. 79. The timing of molting for the four large larvae is as follows: 1) from 10.15 to 10.45 (30 min.); 2) from 13.00 to 13.50 (50 min.); 3) from 14.00 to 15.25 (1 h 25 min.); 4) from 15.10 to 16.50 (1 h 40 min.). The three pygmy larvae died before molting. The molting of the fourth large larva is given here in detail. Illustrations of the second molting are referred to, because the first and second molting are very similar.

15.10:	A shortened, compressed larva curved to resemble a letter C (Fig. 8 A). Earth particles stick to the brilliant skin. Does not move, but tapping, and flashing lights, produce quivering responses
15.23:	Body convulsions: swelling waves starting caudally and moving towards the head rupture the division between the two prothoracic plates; vigorous pulsation of the forehead, and rupture of the λ-formed molting seam of the head capsule (Figs. 8 B, 14 A)
16.10:	Vigorous convulsions at intervals of 5, 5, 10, 10, 10, 11, 12, 17, 18, 19 seconds, and strong pulsation of forehead; the rupture extends caudad and the skin starts withdrawing ventrad, forming whitish longitudinal folds at the sides

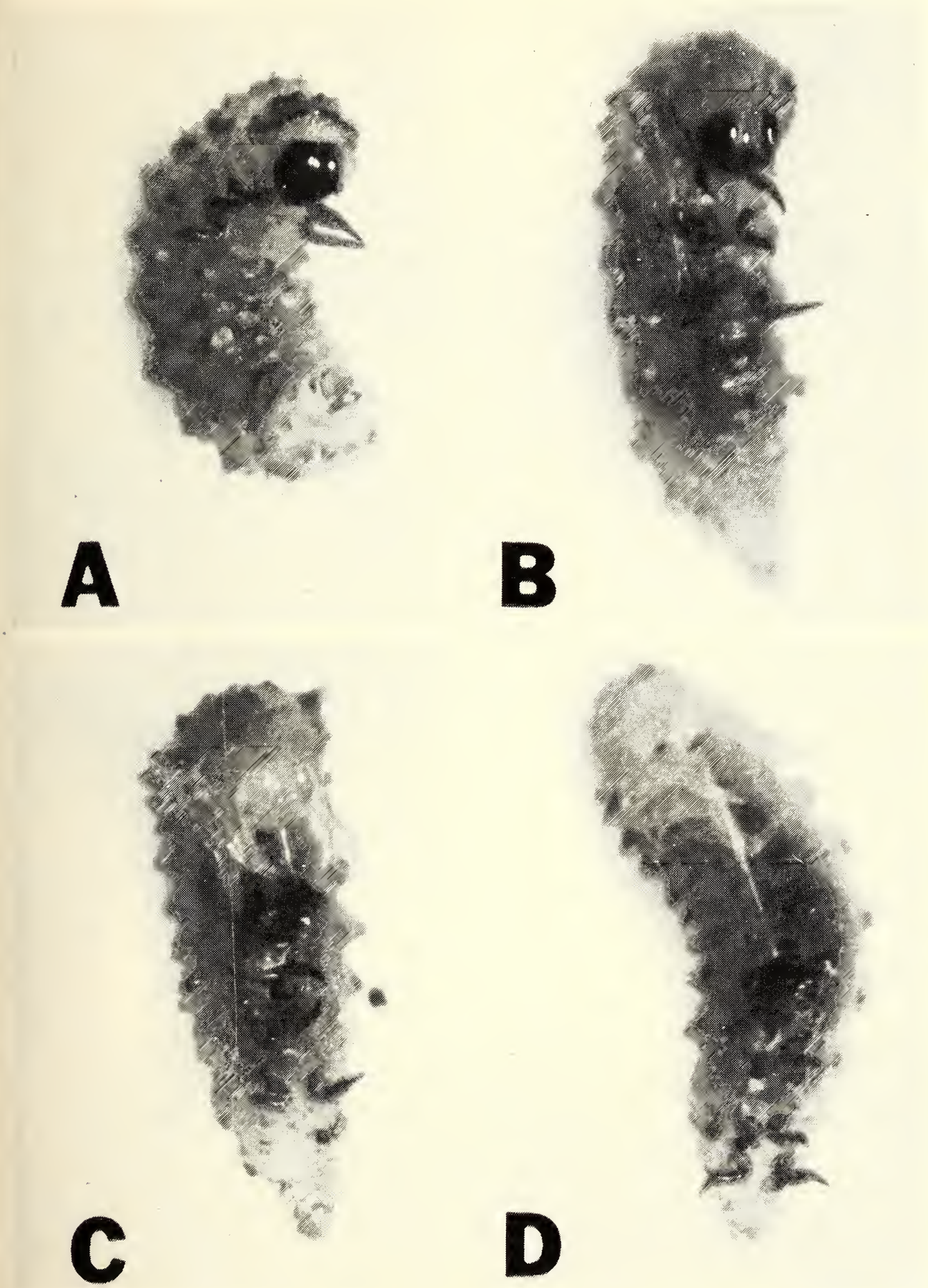

Fig. 8 A to D. Molting of a second instar larva. – A. 17.35: Position C. – B. 18.20: A wave arisen at the caudal end has reached and swollen the prothoracic region. The old skin has been ripped open dorsally, and the split proceeds to the head capsule which opens along its λ-shaped molting line (cf. Fig. 14 A). – C and D. 18.22 to 18.30: Oesophageal exuvium drawn out from the mouth. – Magnification 17×.

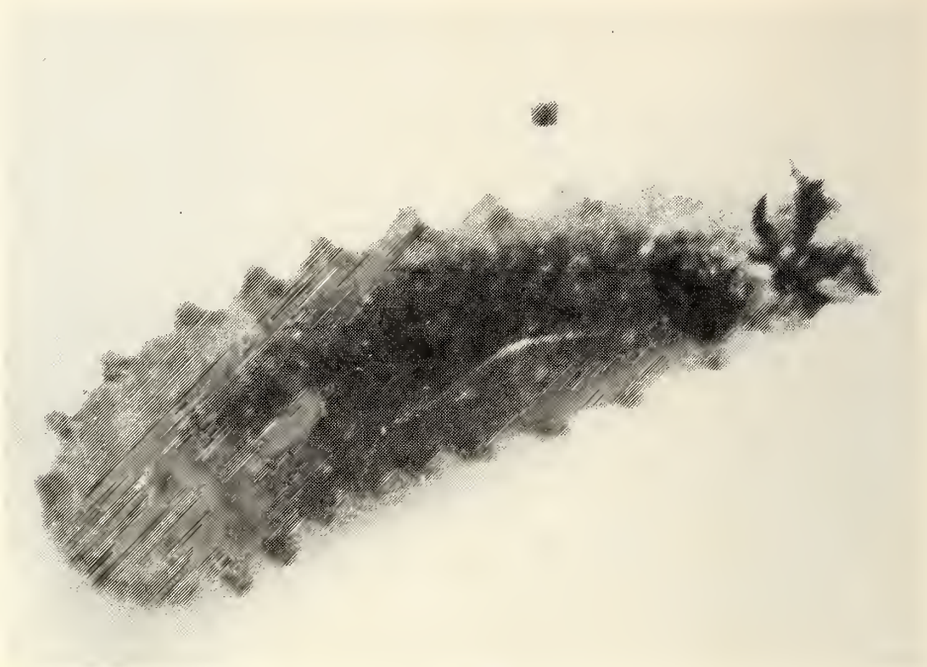

Fig. 9. Continuation of Fig. 8. – 18.32: Oesophageal exuvium completely out. Old skin pushed back to the anal region, where it remains hanging until walking removes it. – Magnification 17×.

16.12: Head free; straightening from its position C, the larva draws out of its mouth an oesophageal exuvium in form of a yellowish string extending about 2.7 mm (Fig. 8 C, D)

16.20: Pulsations and lateral flexions of the body drive the old skin caudad; position C continues

16.24: The oesophageal exuvium separates from the new mouth, remaining attached to the old head capsule (Fig. 9)

16.45: The old skin attached to the end of the larva. The head is yellow, the main body color yellowish-reddish, the prothoracic and anal shields still unpigmented

16.50: The old skin was dropped when the larva started walking. No anal exuvium was observed

17.30: Head light olive, center line black

18.45: Head dark olive, with black spots in the forehead

19.15: Head brilliant black

6. VII. 79 9.40: Anal and prothoracic shields gray; the larva is eating.

Duration of the second instar was reliably determined in 6 cases: 5, 6, 7, 7, 7, 9 days, averaging 6.9 days. The eating rate per day per larva was determined in three samples of sister larvae (in parentheses: days/number of larvae): 0.16 (9/7), 0.22 (6/2), and 0.29 (7/12) cm^2. Full grown second instar larvae measured about 9 to 10 mm in length (walking).

2.2.5 Second molting

This is a process so similar to the first molting that we omit a case history. Figures 8 and 9 are taken from a second molting. Fig. 10 shows how the oesophageal exuvium

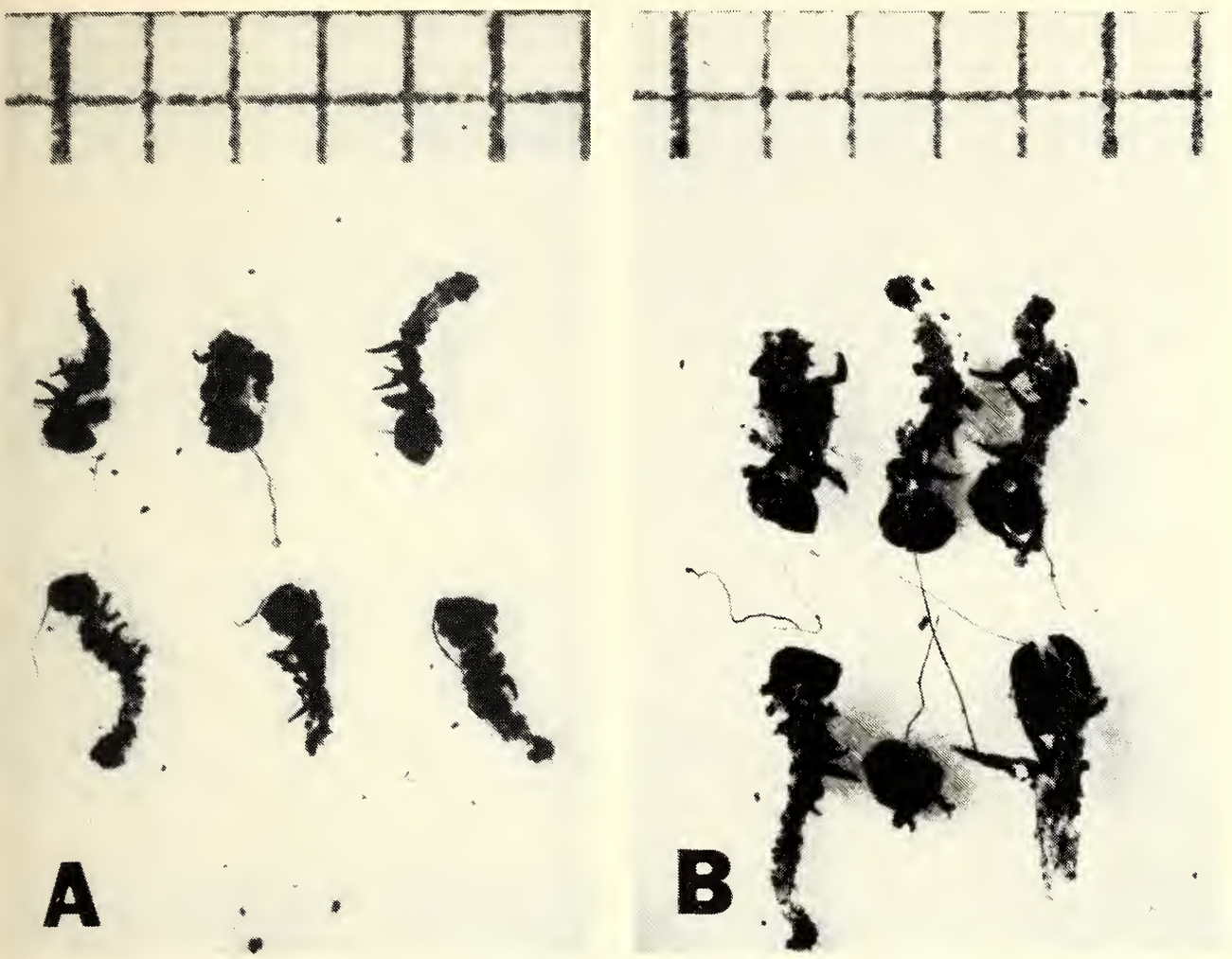

Fig. 10. Skins of the first (A) and second larval molting. Oesophageal exuvium threads attached to the mouth of each skin. – Scale 2 mm².

sticks to the abandoned skins of both moltings. A recognizable anal exuvium thread was never seen in this species. Bypassing observations in Brazil and Puerto Rico (Virkki 1981) showed that an anal, and not oesophageal, exuvium thread is drawn in the moltings of *Omophoita annularis* Ill. and *O. cyanipennis* F., respectively. Failure of detaching the old skin from the anal region is the most common sign of an abortive molting in *A. bicolor*. The anal region becomes usually swollen thereby.

2.2.6 Third instar larva

Duration of this instar varies much. We have only four determinations made on this: 8, 9, 21, and 28 days. Feeding rate also varies much (parentheses as before): 0.16 (28/1), 0.19 (8/6), 0.29 (21/1), 0.56 (18/1), and 0.67 (2/7) cm² per day per larva. Food is taken in the first week, and soon thereafter the larva might be ready for prepupation, provided that the conditions are satisfactory. If they are not (like too little soil in the dish), the larva keeps wandering until it turns a prepupa on the soil. Before this, it may even take food again. In optimal conditions, this instar probably does not exceed 10 days in duration.

From the beginning, this instar is more industrious and terricolous than the preceding ones. Instead of spending all their postfeeding lethargy periods hidden on the soil, the third instar larvae penetrate to crevices and even improve them by excavating.

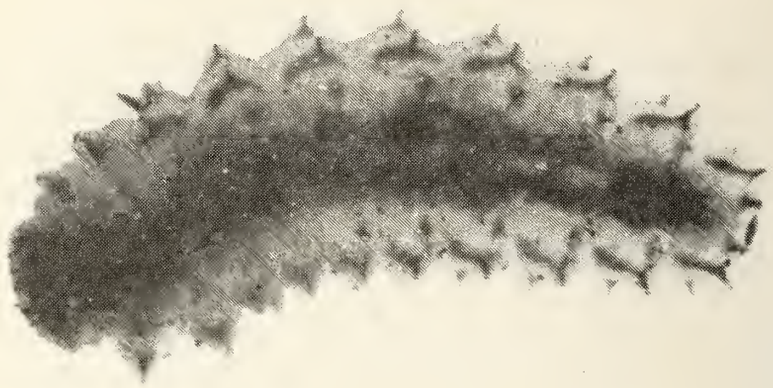

Fig. 11. Fully grown third instar larva seen from the top. Magnification 20×.

The prothoracic and anal shields remain almost similar in color as the main body. Blake (1927) reported the same for a larva of *Oedionychus gibbitarsis;* apparently the larva was of the III instar. Because the body size varies much in all three instars, the pigmentation of these shields remains the best instant criterion for determination of an instar.

A third instar larva (Fig. 11) reaches 12 mm in length, and more if walking. Weight of eight sister larvae (Fig. 1) was as follows: 0.059, 0.059, 0.058, 0.057, 0.051, 0.040, 0.027, and 0.013 g.

The long lethargy periods at least partly explain the enigma why Oedionychina larvae are so seldom met in nature. In 20 years of almost weekly collection of *A. bicolor,* Virkki (1981) has seen only about half a dozen larvae, all in the height of about 1 to 1.5 m on *Clerodendron* bushes. Despite of wiping thousands of *Omophoita cyanipennis* adults from the same bushes and from *Phyla nodiflora,* never has its larva been caught; and yet it is easy to produce them in cages, where they do climb on the hostplant. Apparently the larvae are adapted to make only one feeding trip per instar to the foodplants, most of the time being spent in lethargic aggregations on the ground. If the feeding trip would be nocturnal, the larvae would be better protected against lizards etc., but all laboratory observations favor a diurnal activity.

2.2.7 Formation of the pupal cell

Third instar larvae 8_4 days old start preparing their pupal cells. We cite a case history:

11. VII. 79 11.30: Six larvae, one small, 5 very large:
No. 1. In an excavation since yesterday, 30% of the body visible
No. 2 After rejecting 2 natural crevices, entered the soil
No. 3 Invisible in the earth
No. 4 Accepted and improved a natural crevice
No. 5 On the surface
No. 6 The small one walks and excavates much but abandons the excavations
Follow-up, with special regard to the larva No. 5:

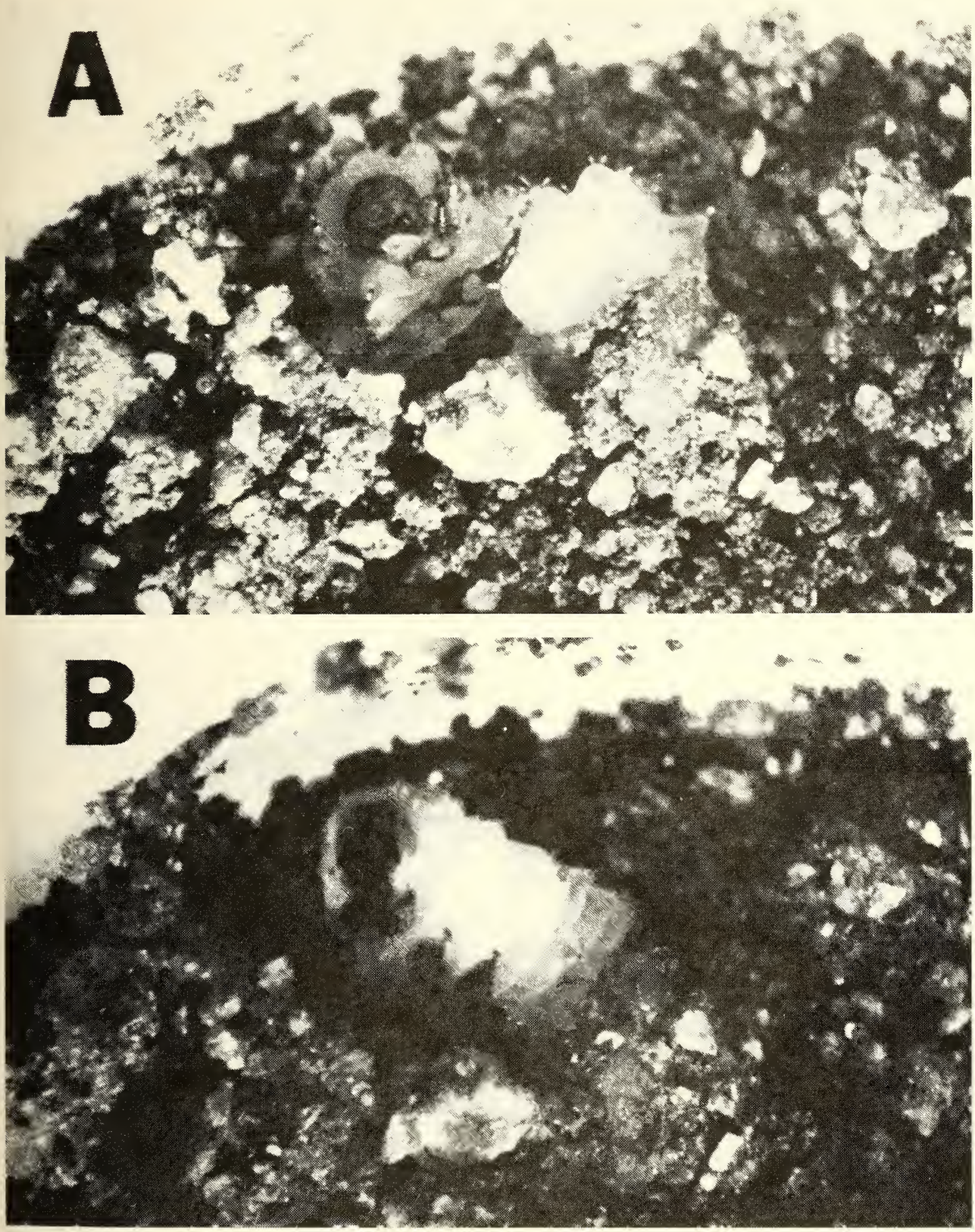

Fig. 12 A and B. A third instar larva closing its pupal cell. – A. Adding a small stone to the rim. Reduced space forces the larva to a curved position. – B. Taking saliva-moistened clay from between the first pair of legs. – Magnification 11×.

12.10: Entering the soil through a natural crevice between loose earth blocks

13.00: After making a horizontal U turn, returned to surface

13.25: Was found excavating in solid earth; swelling waves reaching the forebody helped in the job of penetrating, and widened the excavation; finally made a vertical U turn within the excavation, remaining inside, head up

17.00: All larvae under earth

13. VII. 7.30: All 5 large larvae surfaced again, and ate 1 cm^2

12.00: Two remain on the surface

14.10: One remains on the surface

15. VII. 8.00: Two large larvae on the surface; 3 cm^2 has been eaten. One entered an excavation and started closing it (Fig. 12): Abundant saliva started flowing from the mouth down to an area before and between the first pair of forelegs; with its mouth, the larva placed a piece of clay in this area, maintaining it between the basal segments of the legs; from there, it took small chunks of moist clay to its mouth and deposited them to the rim of the opening of the excavation. When all the clay had been used up, the larva made some hesitating movements, then picked up the next piece of earth, placed it between the forelegs, etc. During these observations, the larvae also made several full turns within the cell, plastering its walls with the mixture of saliva and earth (Fig. 13)

13.45: The cell is closed

18.00: The larva which passed the day on the surface, entered an excavation; another larva surfaced

Fig. 13. The same larva as in Fig. 12, seen through a petri dish wall when plastering the inside wall of its closed pupal cell. – Magnification 11×.

16.–18. VII. 9.00: Larvae have still visited the surface; 1 cm^2 was eaten

15.00: All larvae in the earth. Exposed by forceps the pupal cells were ovoid in shape, about 5 and 8 mm in short and long diameter, respectively, the upper end 1 to 2 mm from the earth surface.

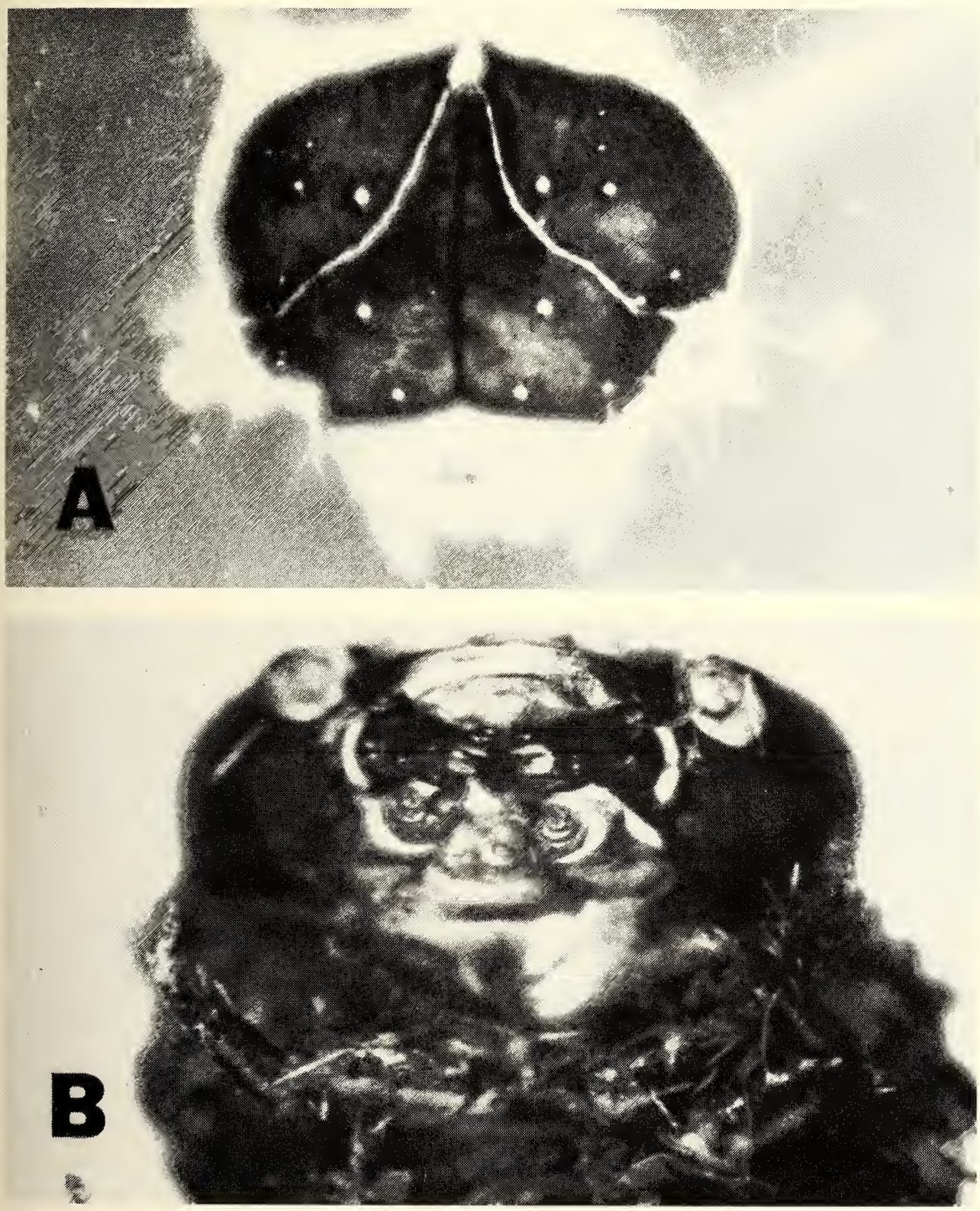

Fig. 14 A and B. Abandoned skins. – A. Head capsule of a second instar larva showing ocelli, the middle line, and the λ-shaped molting line. – B. Anterior end of a prepupal skin. No oesophageal exuvium thread. – Magnification 97×.

The earth-entering period thus took 8 days and was individually very variable. Other case histories suggest that larvae that keep wandering on the surface longer, lose their capacity of saliva excretion, and cannot prepare their pupal cell. They grow smaller, their skin turns yellow, their walking first becomes difficult, then stops, and they turn prepupae on the surface. Such exposed prepupae or pupae were never found in nature nor in our cage cultures. They seem to be a product of suboptimal conditions in the petri dishes.

2.2.8 Prepupa

We followed through glass the progress of a larva which had made its pupal cell adjacent to a petri dish wall. Exceptionally, apparently influenced by the form of the dish wall, this cell was made horizontal.

10. IX. 79	7.30:	A third instar larva just closed the cell and remains curved in order to fit inside; occasionally turns counterclockwise (as seen from the head)
12. IX. 79	7.30:	Notably shortened, now fits almost straight in the cell; still turns around occasionally. Paled to yellow, it is prepupa now
13. IX. 79	18.25:	Convulsion waves passing through the body from the end to the head
	18.27:	A violent contraction and change of position. A notable swelling due to a liquid separating the well visible pupal skin from the larval one. Dorsal vein strongly pulsating
	18.35:	Brief movements of the caudal tip
15.–16. IX. 79	:	Immobile.

Because the above prepupa was accidentally lost, we continue with another case history:

21. I. 80	12.30:	A prepupa in its cell opened for observation; reacts by quivering to knocks and flashing lights; 5 contraction waves pass through the abdomen; heavy swelling of the body (Fig. 15 A)
	14.00 to 15.40:	Contractions 1/min. in the thoracic region
	19.30:	No reaction to knocking; swelling disappeared because of loss of the liquid between the skins (Fig. 15 B)
	21.00:	Abdominal contractions at a rate of 1/min.
	21.30:	Larval skin ruptured at the λ seam of the forehead; the abdomen, bending mostly bachwards, showed pulsating waves. The ruptured skin was pushed caudad. White (tracheal?) threads were thereby molted (Fig. 15 C)
	21.35:	The pupa was free (Fig. 15 D)
	21.50:	Old skin totally packed near to the abdominal tip. No exuvium strings were seen (Fig. 14)
22. I. 80	7.40:	Notable shortening of the pupal body.

The first case history suggests a relatively long age, over 6 days, for the prepupa. We have indeed counted 8 days for a prepupa that had formed on the surface. But in four opened pupal cells, this phase passed in two days, and we believe this is closer to normal. Furth (1982) reports much larger, humidity-depending variation in the duration of diapausing *Blepharida* prepupae.

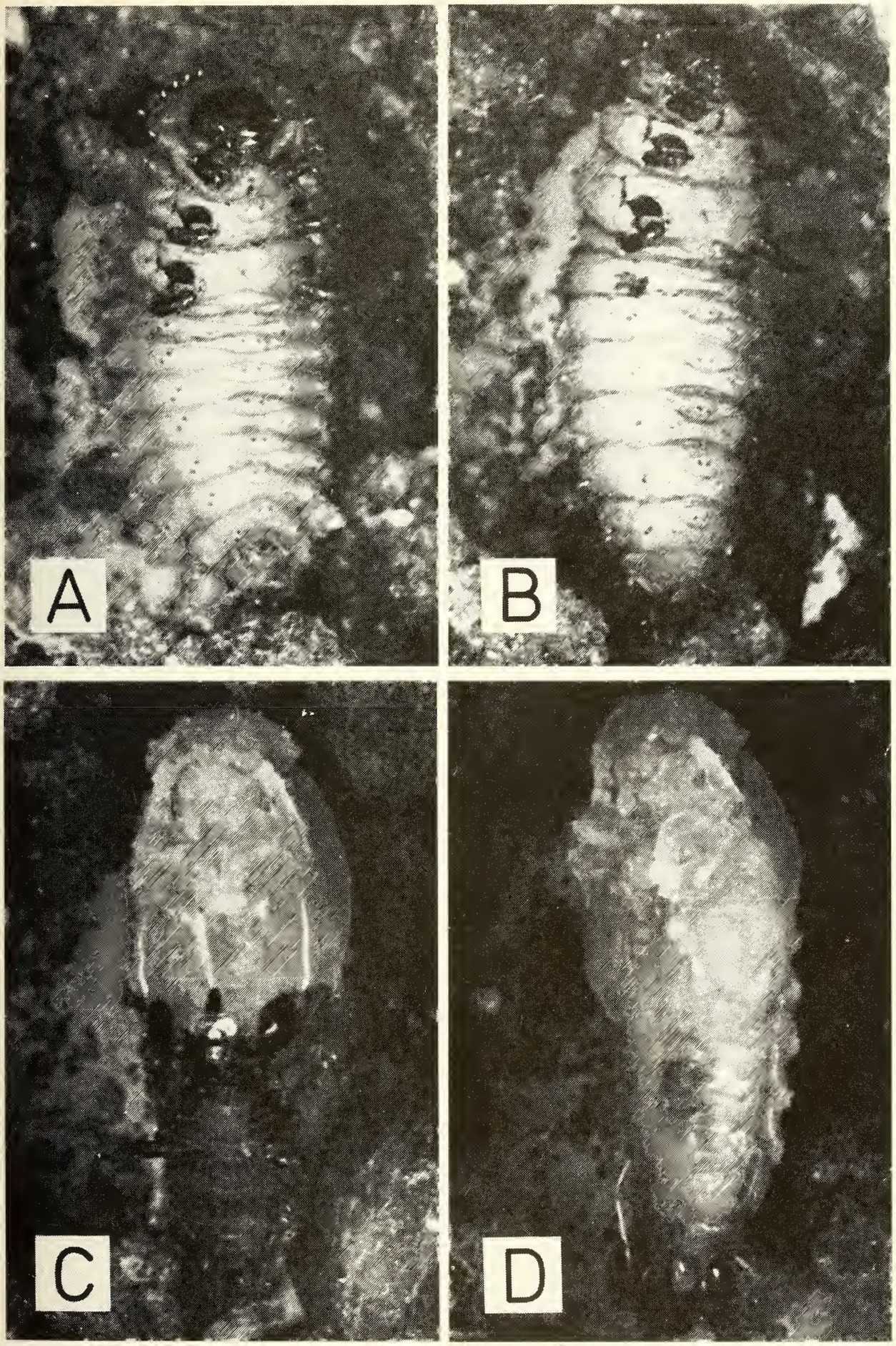

Fig. 15 A to D. Molting of prepupa to pupa. – A. 14.05: A starkly swollen prepupa. – B. 19.30: Liquid between the old and the new skin lost. – C. 21.30: Molting process. – D. 21.35: Molting finished. Obs. white strings (bundles of tracheae?) in C and D. – Magnification 16×.

2.2.9 Pupa and young adult

The pupa (Fig. 16) is about 7 mm long and resembles in structure the *Altica* pupae (Woods 1918). We cite a case history:

Fig. 16 A and B. Pupa in its cell, prepupal skin at the bottom. – A. Six days old, with an incipient pigmentation of the eyes. – B. Nine days old. Eyes dark, incipient pigmentation of femurs. – Magnification 16×.

12. II. 80	8.00:	A yellow pupa of 1 day
14. II.	7.20:	Deeper yellow; a black spot appeared in the IV antennal segment
17. II.	7.30:	Incipient eye pigmentation (Fig. 16 A)
18. II.	7.30:	Eyes pale chocolate colored
19. II.	11.45:	Eyes pale chocolate, mandibles reddish brown
20. II.	7.30:	Eyes dark chocolate, mandibles reddish brown, incipient pigmentation of hind femurs (Fig. 16 B)
21. II.	7.20:	Eyes black, mandibles as above, hind femurs dark except for the proximal halves (like in Fig. 17 A)
22. II.	9.00:	As above, but mandibles move when touched; antennae brown
	14.10:	Flashing lights provoked slight abdominal convulsions
	17.30:	Abdominal pulsations at a rate af 40/min.; mouth parts moved spontaneously

19.00: Pulsations continued; the beetle turned spontaneously its head and nodded with its pronotum; mouth parts moving

20.10: Pulsations continued; lively movement of mouth parts

21.40: Left hind leg and right foreleg free

21.45: Most legs free; slow contractions/extensions of body (like in Fig. 17 B)

21.53: The pupal skin further ruptured at the forehead and slid over the face; rigid straightening of legs and opening of mandibles (like in Fig. 17 C)

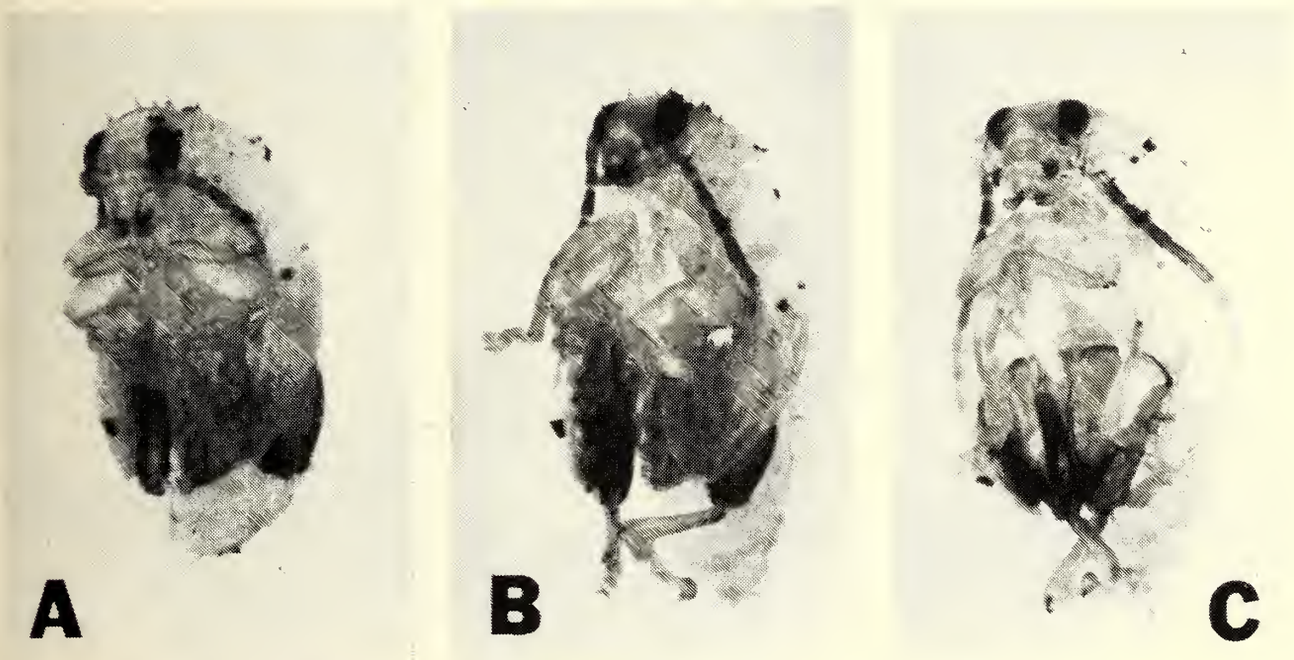

Fig. 17 A to C. Molting of pupa to adult. – A. 9.10: Pupa 10 days old. – B. 9.45: Legs and antennae partly free, elytra moving dorsad. – C. 10.00: Stretching of the body, legs extended, mouth parts gaping. – Magnification 16×.

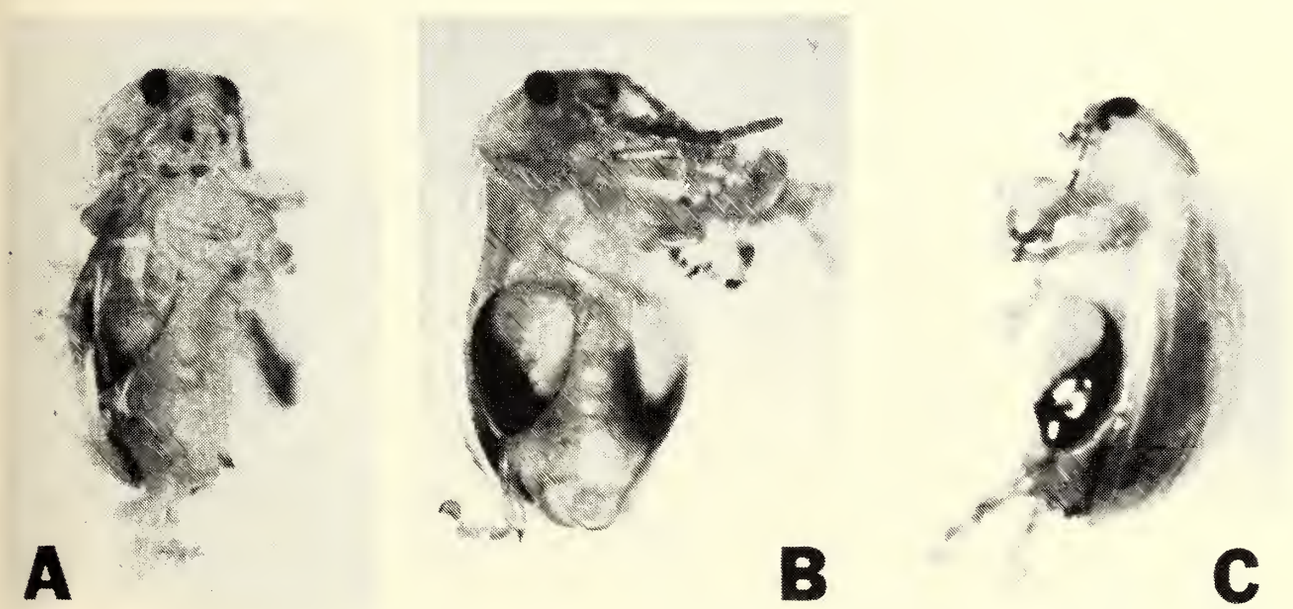

Fig. 18 A to C. Continuation from Fig. 17. – A. 10.12: Pupal skin still attached to the right antenna, right foreleg, and to the tip of abdomen. – B. 10.24: Last struggle, to free right antenna and foreleg. – C. 10.47: Finally free. – Magnification 16 ×.

	22.00:	Legs moved lively pushing the skin back; elytra extended but still pale yellow; bowing of the head (like in Fig. 18 A, B)
	22.07:	Very deep bowing continued at a rate of 4/min.
	22.12:	Telescopic pulsation of abdomen
23. II.	10.25:	Elytra straw colored; distal half of the hind femurs still pale yellow. The new male (like in Figs. 18 C and 19) stays immobile in its cell
24. II.	7.25:	Fully pigmented, left the cell perhaps prematurely, because of the artificial opening; ate about 0.5 cm^2 during the day.

Fig. 19. A fully pigmented young female still in its pupal cell. – Magnification 16×.

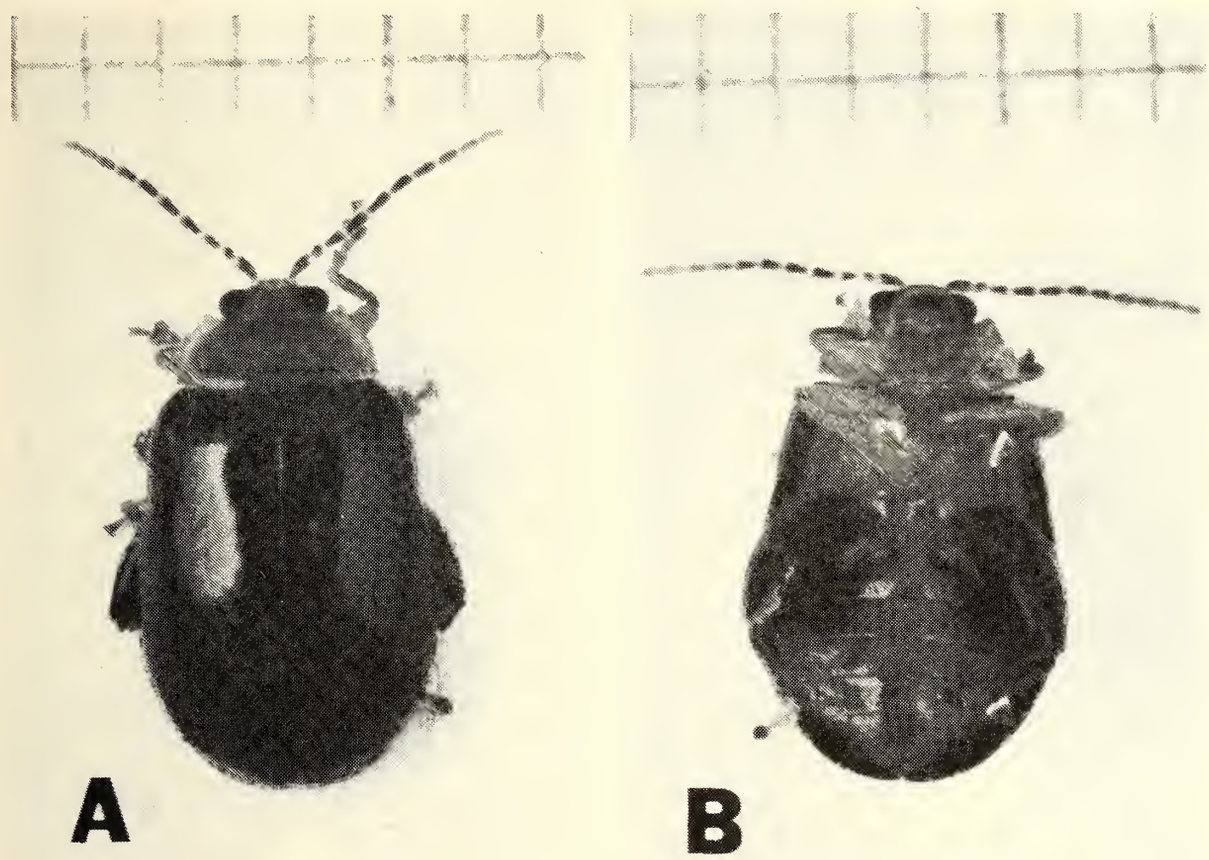

Fig. 20. The female of Fig. 19 after having left its pupal cell, under CO_2 narcosis. – Scale: mm^2.

Fig. 21. A teratological case: permanently swollen left wing. – Scale: mm^2.

We have made 7 reliable observations on the duration of the pupal stage: 8, 9, 10 (5 cases) days, averaging 9.6 days. The young adult (Fig. 20) leaves the pupal cell at the age of 1 or 2 days. Opening out of the cells for observation may have affected this statistics.

2.2.10 Teratology

Among 10 young individuals observed in detail, three were exceptional: One male emerged in 21. VII. 79 had two small holes in its left elytron. Another male belonging to the same cluster emerged in 3. IX. 79 with an oedematic right wing that prevented the elytron of the same side from closing. The defect was permanent (Fig. 21). Another male emerged in 28. VII. 79 could not completely close its elytra.

All these beetles spent their whole metamorphosis in the petri dish cultures.

Conclusions

In general terms, the metamorphosis of *Alagoasa bicolor* resembles that of *Altica* spp., as described in much detail by Woods (1918). The main difference is that the tropical *A. bicolor* lacks diapause, having thus reduced embryonal, prepupal, and/or adult stages. Also the larval behavior is different, the *Altica* larvae spending all the time on the foodplant, the *Alagoasa* larvae on the ground.

Woods (1918) observed molting of the both extremes of the digestive tract in *Altica ulmi*. The finding that only one exevium thread is prominent in our Oedionychina, the oesophageal one in *Alagoasa*, and the anal one in *Omophoita*, deserves more study as a probable distinguishing mark between the Oedionychina genera. Pigmentation of prothoracic and anal shields is a better criterion for a larval instar than in *Altica* spp., where the variation is more extensive.

According to our observations, the approximate timetable of the metamorphosis of *Alagoasa bicolor*, from oviposition to freely moving, fully pigmented adults is as follows:

Eggs	10 days
Larva I	8 days
Larva II	7 days
Larva III	11 days
Prepupa	2 days
Pupa	10 days
Subterranean adult	2 days
TOTAL	50 days

An individual consumes about 5 cm^2 of *Aegiphila martinicensis* leaves during its larval life. This and the above statistics is still debatable, because our material was scanty and the conditions suboptimal.

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