ends of the gene were removed prior to construction of phylogenetic tree. Protein-coding sequences were translated to amino acids using DNASIS for confirmation of alignment. The COI regions of other lepidopterans that corresponds to the amplified COI sequence of *O. fuscidentalis* were obtained from GEN Bank database. The COI sequences were analyzed using neighbor-joining (NJ) method. Stability of NJ tree was assessed via bootstrapping over 1000 replicates. Tree Vies PPC (Aladdin Systems, Watsonville, CA) was used to construct NJ tree.

Statistical analysis

Data were statistically analyzed with 2-way ANOVA. Analysis of head capsule width was performed using JMP (ver. 3.02; SAS Institute, Inc.).

Annual changes in climate in Chiang Mai area

The meteorological records of 9 years from 1988 to 1996 were provided by Meteorological Observatory, Chiang Mai, Thailand. Monthly precipitation of less than 100 mm is considered to be the threshold of drought in the tropical region (Whitmore, 1984). According to these criteria, the monthly changes in precipitation in Chiang Mai (Fig. 1) clearly show a wet-dry cycle: a dry season from November through April and a rainy season from June through October. The dry season is divided into two seasons according to temperature, a cool season (winter) from November to February and a hot season (summer) from March to June. Accordingly, there are three seasons, wet season followed by dry winter and dry summer.

RESULTS

Identification of *Omphisa fuscidentalis*

The nucleotide sequence of the COI region amplified by PCR (Fig. 2A) showed that there was only one nucleotide difference, A or G of 438 nucleotides determined: at position 312 where the nucleotide was A in larvae from the bamboos, *D. Hamitonii*, *B. blumeana* and *G. albociliata*, or G in those from *D. membranaceus* and *B. nutans*. This single replacement of nucleotide did not affect on the amino acid residue. The deduced amino acid sequences of the amplified COI region were identical among larvae collected from 5 different bamboo species. Accordingly, we concluded that the larvae found on different bamboo species belong to the same species.

To confirm that the amplified DNA is a region of COI, we compared the gene sequence and the deduced amino acid sequence with those of *Manduca* COI (Frohlich *et al.*, 1996). As seen in Figure 2B, The homology of the amplified region between *O. fuscidentalis* and *M. sexta* was 83% for the nucleotide sequence and 93% for the deduced amino acid sequence.

The phylogenetic tree (Fig. 3) was constructed with the present data and the sequences of the same region in other lepidopteran species. The NJ tree indicated that *O. fuscidentalis* fell in the same cluster as *Spodoptera*, *Manduca* and *Antheraea* since bootstrap value was 76%.

Estimation of number of larval instar

Figure 4 shows frequency distribution of width of the head capsules which were collected from 17 bamboo shoots. The first and second peaks were clearly observed but the peaks were not clear in three clusters ranged between 1-1.5, 1.5-2.4 and 2.4-3.3 mm. In addition, we measured the width at different intervals according to the width: the width was measured at every 0.0263 mm if it was less than 2.6 mm and at every 0.05 mm for the width not less than 2.6 mm (Fig. 4). Thus, we standardized the distribution in common logarithm, converted each peak to a normal distribution and calculated the mean value for each peak (Table 1). Then the values of head capsule width in common logarithm was plotted against the putative number of instars (Fig. 5). The curve gave a good correlation coefficient (r^2=0.998) and well fitted to Dyar's law and therefore we concluded that number of *Omphisa* larval instars is five. The ratio was calculated to be 1.51 from the curve gradient of 0.180 in Figure 5.

In Figure 4, the peaks for third, fourth and fifth instars appeared to be broad. Such broad peak indicated a sexual dimorphism in the larval size and thus we tried to plot the values of first and second peaks for the third through fifth instars after converting the values in common logarithm. Since a single peak was observed for each of first and second instars, these peak values were directly used for depicting two lines in Figure 6. Each peak values were on a straight line and each line gave a good correlation coefficient (r^2) of 0.997 for upper line (larger width) and 0.999 for lower line (narrower width).

In order to confirm the sexual dimorphism, we determined the sex of 100 diapause larvae by dissecting and confirming the existence of ovary or testis and measured the head capsule width of the same larvae. Figure 7 shows the frequency distribution of head capsule width of male and female larvae. The head capsule width in females was significantly larger than in males (p=0.0000), showing the sexual dimorphism in the head capsule width in the mature larvae. Mann-Whitney U-test showed that the population of 100 larvae is not significantly different from that of 5th instars used for depicting Figure 4 (p = 0.84). The mean values for male ($\log_{10}$ 0.421) and female ($\log_{10}$ 0.467) were therefore replaced with those for the 5th instar in Figure 6. The newly depicted curves gave a correlation coefficient (r^2) of 0.996 and 0.999 for male and female, respectively. This clearly showed that the larger peaks as indicated with open triangles in Figure 4 were for females' capsules while smaller ones (filled triangles for third, fourth and fifth instars) are males' capsules.

Body weight and head capsule width

Figure 8 shows the changes in the wet body weight of larvae and head capsule width after maturation. Mean body weight was 0.61 g soon after larval maturation in October and then decreased continuously until February ($y = -0.045x + 0.703$, $r = 0.988$, Oct vs Dec, $p<0.0001$; Dec vs Feb, $p<0.002$). Body weight increased in March ($p<0.01$) and then again sharply decreased in May ($p<0.0001$). From September to May, larvae lost approximately 47% of their wet weight. Head capsule width did not change significantly during 9 months ($p>0.1$). There was considerable variation both in body weight and head capsule width among individuals in every month (Fig. 9). Head capsule width varied from 2.5 to 3.0 mm. However, no correlation was found between the head capsule width and body weight ($r=0.179$). This may indicate that the variation in head capsule width occurred within the same larval instar.

Gut observation

Gut contents were observed for larvae in diapause. In larvae collected in February, there was no solid material in their midgut. Wet weight of gut content was 21 ± 1 mg (n=3) which was 3.5 ± 0.3 % of larval body weight (595 ± 23 mg). In the gut of the bamboo borer larvae, there was no solid materials except in anus where a mass of fibrous materials was found to shape a plug in anus. To estimate the loss of gut contents during the diapause, larvae collected in January was kept at 25 °C under high humidity for one month and the gut contents was measured. In those larvae, gut contents was 9.3 ± 3.7 mg (n=3) which was 1.9 ± 0.8 % of larval body weight (504 ± 34 mg).

For comparison, we measured the gut contents of the silkworm, *Bombyx mori* at the time after cessation of feeding but before purging gut contents. The aqueous contents was 14.2 ± 2.4 % of fresh body weight (3.71 ± 0.12 g; n=6). At this time, no solid piece of artificial diet was found in fore- and mid-gut. Only a piece of frosty feces was observed at the anus.

Changes in protein and fat contents during larval diapause

Larval body weight in May was about half the initial weight. It was therefore interest to determine the changes in fat and protein content throughout the diapause period. As shown in Figure 10, the proportional fat content fluctuated largely month by month: the highest level was found in October (0.201) and the lowest in March (0.048). By contrast, the protein level did not change significantly until January ($p>0.1$, ANOVA), after which it appeared to increase in February, decrease in March and then increase again in May.

Changes in the hemolymph ecdysteroid levels

Hemolymph ecdysteroid titer was determined for larvae collected in September through May and for pupae in June and July (Fig. 11). The titer was low during the larval period but fluctuates in a range from 3 to 22 ng/ml. For the first 3 months, the

titer was less than 3 ng/ml and increased to a peak value of 22 ng/ml in December after which it declined until March. A small peak was observed in April and then decreased again in May. The hemolymph ecdysteroid titer thus showed significant fluctuations but did not increase to more than 22 ng/ml. Accordingly, the titer was maintained at low levels up to May. During the pupal period, the titer increased to approximately 1,700 ng/ml in June and decreased to 770 ng/ml in July, shortly before adult eclosion.

DISCUSSION

Identification of the bamboo borer larvae

For the present study, we monthly collected bamboo borer larvae from natural habitat. The moth of the bamboo borer we used was identified as *O. fuscidentalis* by two taxonomists, Dr. M. Shaffer of Natural History Museum, London and Dr. H. Banzinger of Chiang Mai University. In Chiang Mai area, we found the larvae from more than 5 different bamboo species, *D. membranaceus*, *D. hamitoni*, *B. nutan* , *B. blumeana* and *G. albociliata*. Robinson *et al* (1994) described the distribution of two species of genus *Omphisa* distribute in South-East Asia, and therefore it was possible that the bamboo borer larvae from different bamboos in the same area belong to different species. The nucleotide sequence and the deduced amino acid sequences, however, strongly suggested that all the larvae collected from 5 different bamboos belong to the same species. The NJ tree constructed from the nucleotide sequences of COI region amplified by PCR indicated that *Omphisa* share a cluster with *Manduca sexta* and *Spodoptera ornithog*. This is, however, only a matter of indication because the bootstrapping values were less that 75% inside the cluster.

Larval growth and diapause

Dyar's law shows that the head capsule of caterpillars grows in geometrical progression, increasing in width at each molt by a ratio which is constant for a given species (Wigglesworth, 1972). When this law is applicable, it is possible to deduce the actual number of ecdysis from the cast head capsules. The growth curve for the head capsule width of the bamboo borer showed a very good correlation coefficient with the ratio of growth of 1.51, showing that growth of the bamboo borer fits Dyar's law . The ratio of 1.51 is similar to that for other lepidopteran larvae, *Samia cynthia ricini* (r=1.52) and *Crambus mutabilis* (r=1.44). Accordingly, the number of larval instars was concluded to be five and the matured larvae found from the bamboo shoot in September and thereafter must be the 5th instar.

Head capsule width of insects increases at every ecdysis but not during an intermolt period (Nijhout, 1975; Chippendale and Yin, 1976, Suzuki and Nishimura, 1997). In *O. fuscidentalis*, head capsule width of larvae did not change throughout the 9 month period from September to the following May, showing that the bamboo borer larvae did not undergo an additional larval ecdysis until pupation in the field, and

therefore *O. fuscidentalis* possesses a very long period of larval diapause. During the diapause, larval body weight decreased. When larvae were disturbed, they actively moved. There was no solid material in fore- and mid-gut while a mass of fibrous material was placed like a plug at anus. Such plug-like mass is usually observed at anus before gut purge. Prior to gut purge, such mass which is usually frosty is excreted as a last piece of feces. In addition, their body length shortened prior to pupation in June (unpublished observations), which commonly occurs at the onset of the prepupal period in lepidopteran larvae. Accordingly, all the circumstantial evidences suggest that the larvae entered diapause at the end of the phagoperiod in the last larval instar. The long larval diapause was also confirmed by very low hemolymph ecdysteroid concentrations throughout the diapause period.

Loss of body weight is common in diapause larvae. Prepupae of the Mediterranean tiger moth, *Cymbalophora pudica* spend summer in a summer diapause (aestivation) and lose up to 50 % of their body weight for 3 months. The dry weight of *C. pudica* larvae in aestivation remained stable (Kostal *et al.*, 1998), an indication that the loss may mainly due to desiccation. Larval body weight in *O. fuscidentalis* decreased to about half of the initial weight over 9 months. The small decrease compared with *C. pudica* may be due to the special habitat of the larvae, i.e. inside the bamboo internode where the relative humidity is more than 90% (unpublished observation) and desiccation is less likely. Nevertheless, desiccation may be partly involved in the loss of body weight. Wet weight of gut contents of February larvae was 3.5% of wet body weight. Though we did not weigh the gut contents for September larvae, the weight may be more than 10% of wet body weight because it was about 14% in *Bombyx* mature larvae immediately before gut purge. If this can be the case in *Omphisa*, water of gut contents must be lost during the diapause. In addition, the loss of gut contents was also observed when larvae were kept in an incubator though the container of larvae was kept under high humidity. Accordingly, aqueous gut content could partly cover such desiccation during the long larval period in diapause in *Omphisa*.

Protein content proportional to wet body weight remained at the initial level for the first 7 months except in February. This means that the total amount of protein of individual larvae decreased during this period because wet body weight decreased rapidly in the diapause period. The proportional fat content greatly fluctuated month by month. Although the monthly fluctuation was statistically significant, it is not obvious whether such fluctuations actually occur in a single larva or possesses physiological meanings. The proportional fat content appeared to increase at the end of diapause, similar to the protein content.

An increase in both of proportional protein and fat contents was observed in May, concurrent with a decrease in body weight. May was one month prior to pupation. It is a common feature that the diapause is actually terminated long before developmental events become overt, such as pupation after larval diapause (Yin and

Chippendale, 1973), adult development after pupal diapause (Bowers and Williams, 1964) and egg maturation after adult diapause (Tanaka *et al.*, 1988). Accordingly, the profile of protein and fat levels in April and May may indicate that termination of larval diapause might be initiated in or before April.

Larval diapause in tropical insects

The increase in plant growth stimulated by the rains provides a wealth of new food resources for many phytophagous insects and the availability of food may be influenced profoundly by seasonal rhythms (Denlinger, 1986). The long diapause is, therefore, important in maintaining synchrony between the insect life cycle and the phenology of its host plants in the tropics: diapause is adaptive as a seasonal trait as the depletion of food supply (Tauber *et al.* 1986). Such a situation may be produced in the Chiang Mai area with dry-wet season cycle by the regular occurrence of droughts (see Fig. 1) that deplete the food supply in young bamboo shoots. The bamboo borer larvae feed on the soft inner pulp of the new bamboo shoots. The bamboo produces new shoots in the wet season and the shoots become hard by the end of the wet season. This indicates that larval diapause in the bamboo borer has evolved in response to the depletion of the food supply and thereby larvae survive seasonally recurring adverse conditions.

Diapause in tropical species is often variable and may occur only in a relatively small portion of the population (Tauber et al., 1986). The diapause in tropical insects is mostly facultative diapause in which diapause or non-diapause depends on environmental cues as reported for *Diatraea grandiosella* (Kikukawa and Chippendale, 1983), the flesh flies (Denlinger, 1979), *Chilo* species (Scheltes, 1978) and *Busseola fusca* (Usua, 1973). In *Omphisa*, however, the long larval diapause appears not to be facultative. Omphisa larvae are found in local markets in Northern Thailand through a year except 4 months from June through September. When the larvae collected in October to December were kept in an incubator for months at constant temperature under dark and high humidity, they remained as larvae. Accordingly adult may appear once a year and the larval diapause may be obligatory. It remains, however, to be determined whether the larval diapause is obligatory and what environmental and genetic factors influence diapause of bamboo borer.

Pupation of individual larvae of a single colony appears to occur synchronously since adult development in pupae in one internode was well-synchronized (unpublished observation). This indicates that the break of diapause must be environmentally regulated. The environmental factor that changes largely through a year is monthly precipitation and thus possibly humidity. We kept the larvae collected from the field in laboratory conditions with a high humidity at around 25 °C, but larvae did not pupate for months if collected in October-December. Under the same conditions, the May and June larvae occasionally pupated within a month, but synchronized pupation was not observed (unpublished observation). The habitat of the larvae is inside the internode of

a bamboo culm where the humidity is rather constant. This indicated that the cue might not be humidity. Photoperiod is a common environmental cue to break diapause. The bamboo culm wall is more than 1 cm thick and it may be impossible that light would pass through the wall because the light permeability of the wall was about 1×10^{-9}%/cm (unpublished observation). The remaining possible cue is temperature but changes in temperature is not a reliable cue for predicting seasonally recurring favorable conditions. The factor which is tightly involved in the break of larval diapause in *Omphisa* remains is obscure.

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FIGURE LEGENDS

Fig. 1. Meteorological data from Chiang Mai, Thailand at 19 °N. Top, highest and lowest temperature; middle, precipitation; bottom, highest and lowest relative humidity. Each datum point is a mean with SD of the statistical data for 9 years from 1988 to 1996, provided by Meteorological Observatory, Chiang Mai, Thailand.

Fig. 2. DNA sequence and the deduced amino acid sequence of the mitochondrial cytochrome C oxidase subunit I (COI) region from the bamboo borer larvae collected from 5 different bamboo species (A) and a comparison of the amino acid sequence of the amplified region of COI with that of *Manduca sexta* (B) (Fröhlich et al., 1996). The nucleotide at position 312 as indicated with an asterisk in (A) was A in larvae from the bamboos, *D. Hamiltonii*, *B. blumeana* and *G. albociliata* or G in those from *D. membranaceus* and *B. nutans*. Asterisk in (B) indicates the different amino acids between *Omphisa* and *Manduca*.

Fig. 3. Neighbor-joining tree calculated from an alignment of COI region sequences of 13 selected lepidopteran species. *Drosophila melanogaster* was used as an outgroup. Numbers at a node indicate percentage bootstrap values higher than 75%.

Fig. 4. Frequency distribution of the head capsule width in *O. fuscidentalis* larvae. Head capsules were collected from 17 bamboo shoots in September and October, 1998. Solid and open triangles indicate the peak values for depicting Figure 6. See text for details.

Fig. 5. Correlation of the head capsule width and number of larval instars in *O. fuscidentalis*. Head capsule width is expressed in common logarithm. $y = 0.180x - 0.462$; $r^2 = 0.999$. Thin lines indicate the upper and lower 95% mean value, respectively.

Fig. 6. Indication of sexual dimorphism in the larval growth. Values of head capsule

width as indicated with filled and open triangles in Figure 4 was converted to common logarithm and plotted against the number of instars. The curves for filled and open triangles in Figure 4 are indicated with diamonds and circles, respectively. The correlation coefficient (r^2) for diamonds and circles are 0.997 ($y = 0.194x - 0.459$) and 0.999 ($y = 0.179x - 0.478$), respectively.

Fig. 7. Sexual dimorphism in the head capsule width. Head capsule width was measured and then the larval sex was determined by confirming the presence of testis or ovary. The mean values for females (filled column, n = 46) and males (hatched column, n = 54) were 2.64 ± 0.13 and 2.94 ± 0.12 mm, respectively. p = 0.0000 (Student's t-test).

Fig. 8. Changes in wet body weight (circles) and head capsule width (triangles) of *O. fuscidentalis* larvae from September to May. Each datum point is a mean of 20 mature larvae with SD. The correlation coefficient (r) for head capsule width is 0.186 ($y = 0.009x + 2.71$).

Fig. 9. Correlation between the head capsule width and wet body weight of mature larvae. The correlation coefficient (r) is 0.179 ($y = 0.17x - 0.041$).

Fig. 10. Monthly changes of the proportional protein and fat contents of mature larvae of *O. fuscidentalis* from September to May. The ordinate indicates fat or protein content proportional to g wet body weight. Each datum point is a mean with SD of 3 different determinations.

Fig. 11. Changes in hemolymph ecdysteroid concentration of *O. fuscidentalis* from September to May and pupal stage in June and July. Insert is an enlargement of the data from September to May. Each datum point is a mean with SD of 20 different determinations. Datum point with no SD bar indicates that SD was smaller than the mark size.

Table 1. Various moments for each peak of head capsule width.

	Instar				
Moment	1	2	3	4	5
Number	55	91	154	223	164
Mean value (mm)	0.533	0.768	1.199	1.820	2.774
Standard deviation	0.026	0.056	0.098	0.161	0.184
Upper 95% mean value	0.541	0.779	1.214	1.841	2.803
Lower 95% mean value	0.529	0.756	1.214	1.184	2.745

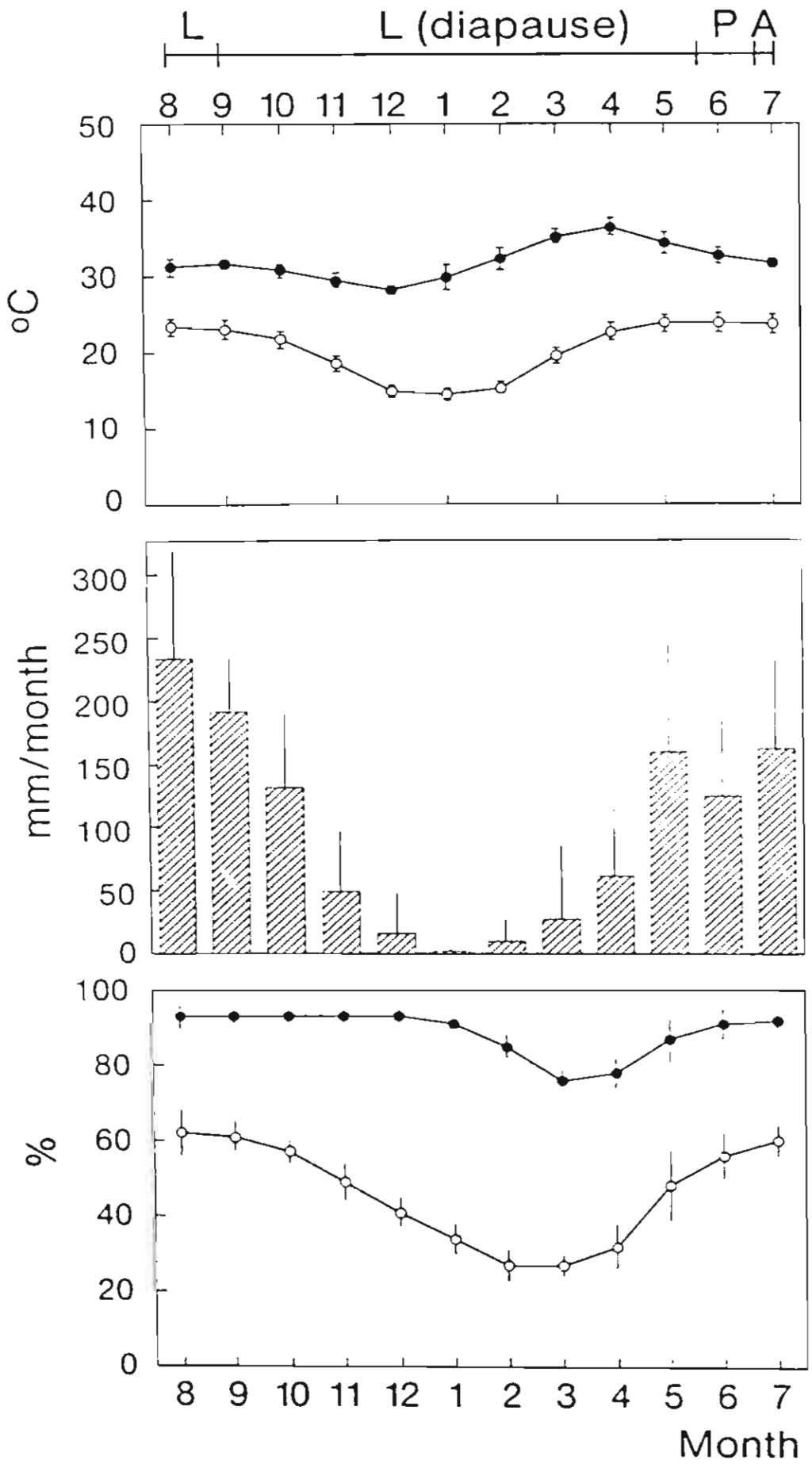
L
L (diapause)
P A
8 9 10 11 12 1 2 3 4 5 6 7
°C
50
40
30
20
10
0
mm/month
300
250
200
150
100
50
0
%
100
80
60
40
20
0
8 9 10 11 12 1 2 3 4 5 6 7
Month

Figure 1

A

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CGA ATA AAT AAT ATA AGA TTT TGA TTA TTA CCC CCA TCT CTA ACT CTT TTA ATT TCA 57
 R   M   N   N   M   S   F   W   L   L   T   P   S   L   T   L   L   I   S

AGA AGA ATT GTT GAA AAT GGA GTA GGA ACT GGA TGA ACT GTC TAC CCC CCC CTT TCA 114
 S   S   I   V   E   N   G   V   G   T   G   W   T   V   Y   P   P   L   S

TCC AAT ATT GCT CAC AGA GGA AGT TCT GTT GAT TTA GCA ATT TTT TCC TTA CAT TTA 171
 S   N   I   A   H   S   G   S   S   V   D   L   A   I   F   S   L   H   L

GCT GGA ATT TCT TCT ATT TTA GGA GCA ATT AAT TTT ATT ACA ACT ATT ATT AAC ATA 228
 A   G   I   S   S   I   L   G   A   I   N   F   I   T   T   I   I   N   M

CGT ATT AAT GGT CTA CTA TTT GAT CAA ATA CCA TTA TTC GTC TGA TCA GTA GGA ATT 285
 R   I   N   G   L   L   F   D   Q   M   P   L   F   V   W   S   V   G   I

ACA GCT CTA TTA TTA CTT TTT TCT TTA* CCT GTT CTA GCG GGA GCC ATT ACT ATA CTC 342
 T   A   L   L   L   L   F   S   L   P   V   L   A   G   A   I       M   L

TTA ACT GAT CGA AAC TTA AAT ACA TCC TTT TTT GAA ACT GCG GGA GGA GGA GAT CCA 399
 L   T   D   R   N   L   N   T   S   F   F   E   T   A   G   G   G   D   P

ATC CTT TAT CAA CAT TTA TTT TGA TTT TTT GGA CAT CCA 438
 I   L   Y   Q   H   L   F   W   F   F   G   H   P
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B

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                          *                   *
Manduca  97 RMNNMSFWLL PPSLMLLISS SIVENGAGTG WTVYPPLSSN 136
Omphisa   1 RMNNMSFWLL PPSLTLLISS SIVENGVGTG WTVYPPLSSN  40

                                                      *
       137 IAHSGSSVDL AIFSLHLAGI SSILGAINFI TTIINMRINN 176
        41 IAHSGSSVDL AIFSLHLAGI SSILGAINFI TTIINMRING  80

           **           *     *     *
       177 MSFDQMPLFV WAVGITAFLL LLSLPVLAGA ITMLLTDRNL 216
        81 LLFDQMPLFV WSVGITALLL LFSLPVLAGA ITMLLTDRNL 120

                 **
       217 NTSFFDPAGG GDPILYQHLF WFFGHP 242
       121 NTSFFGTAGG GDPILYQHLF WFFGHP 146
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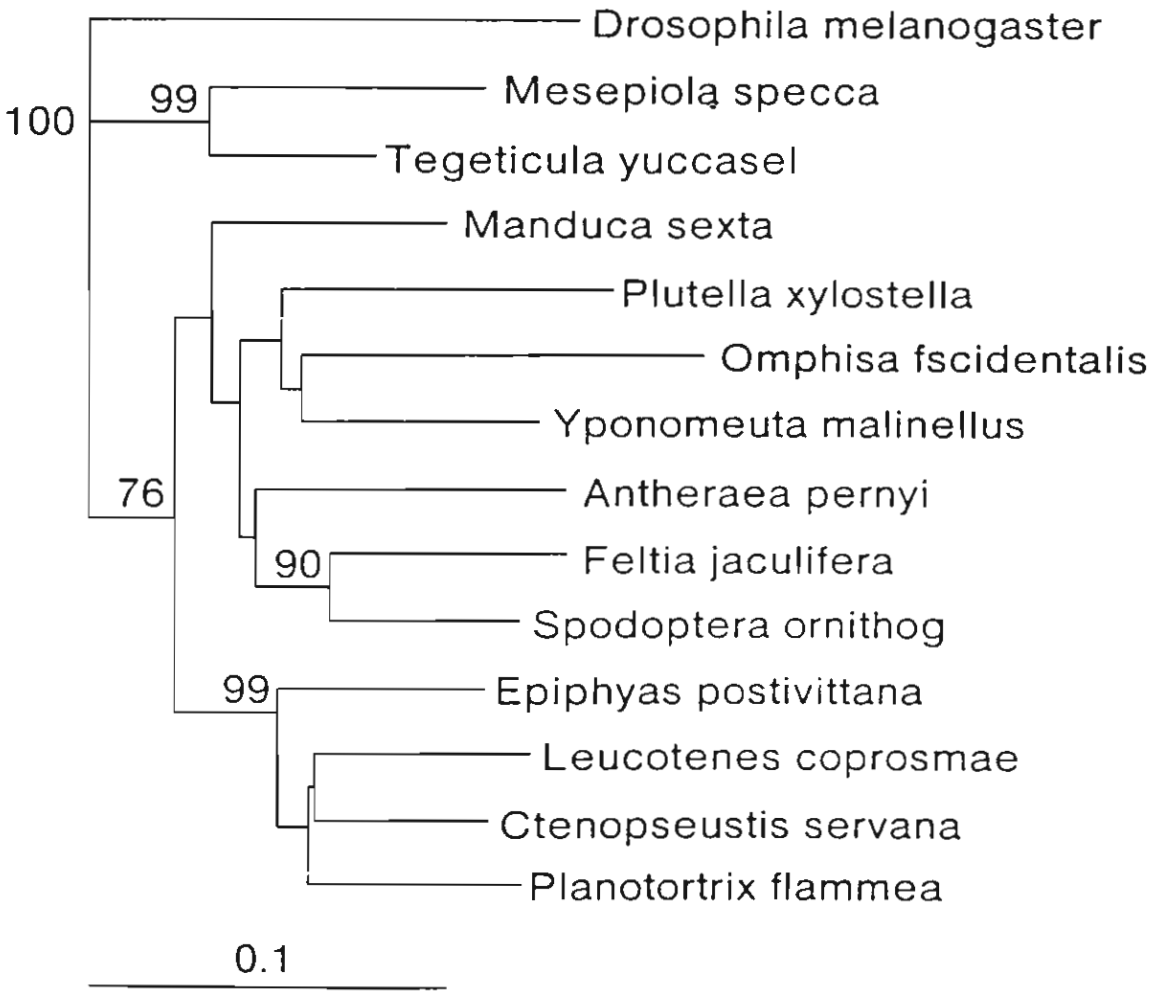
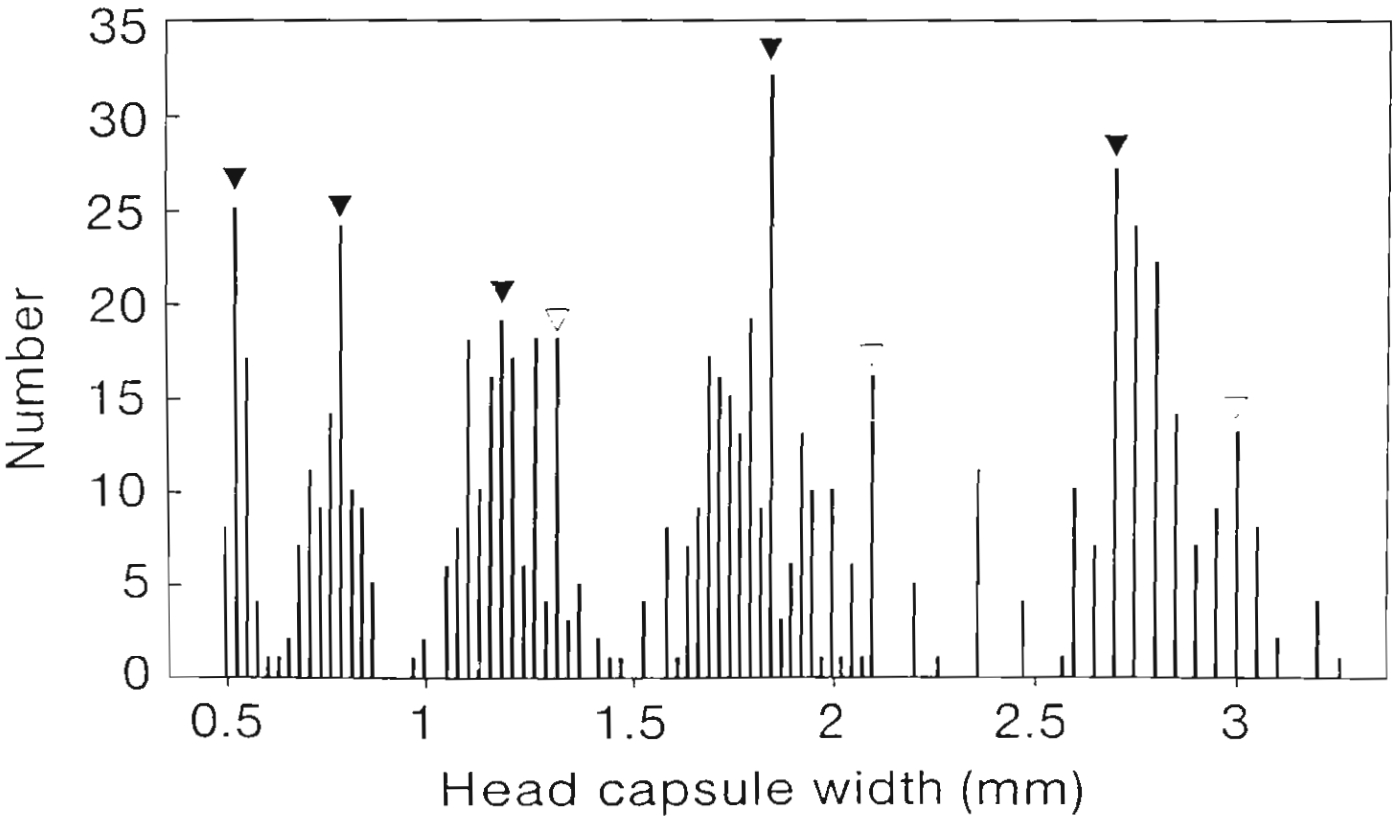

Drosophila melanogaster
Mesepiola specca
Tegeticula yuccasel
Manduca sexta
Plutella xylostella
Omphisa fscidentalis
Yponomeuta malinellus
Antheraea pernyi
Feltia jaculifera
Spodoptera ornithog
Epiphyas postivittana
Leucotenes coprosmae
Ctenopseustis servana
Planotortrix flammea
100
99
76
90
99
0.1


35
30
25
20
15
10
5
0
Number
0.5
1
1.5
2
2.5
3
Head capsule width (mm)

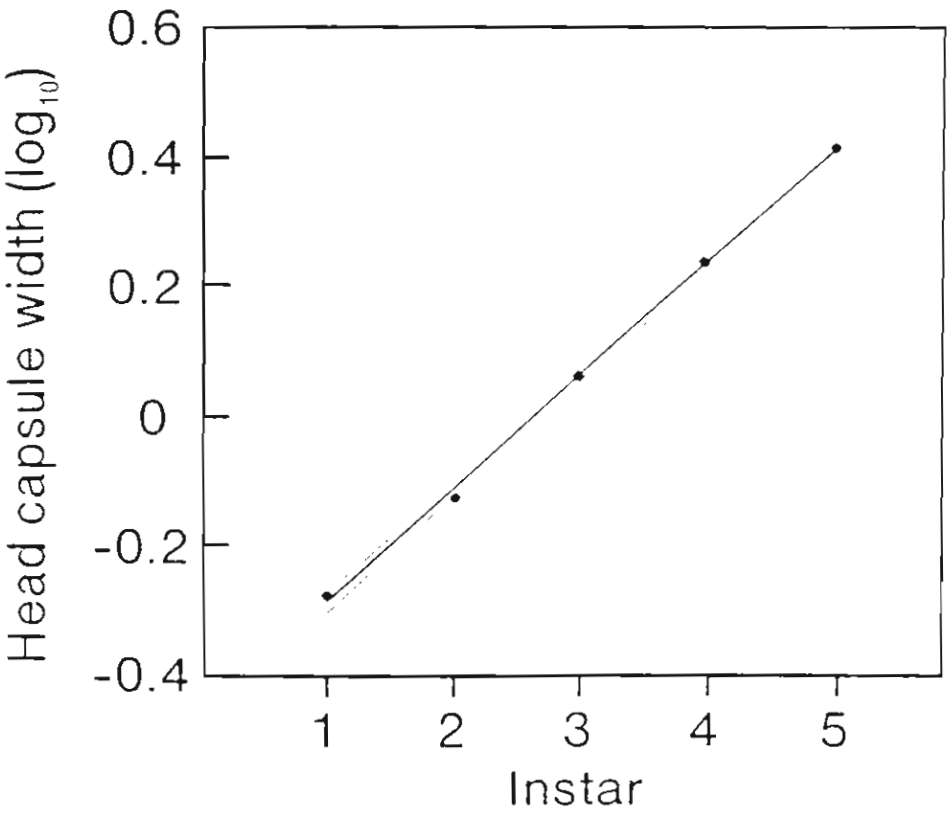
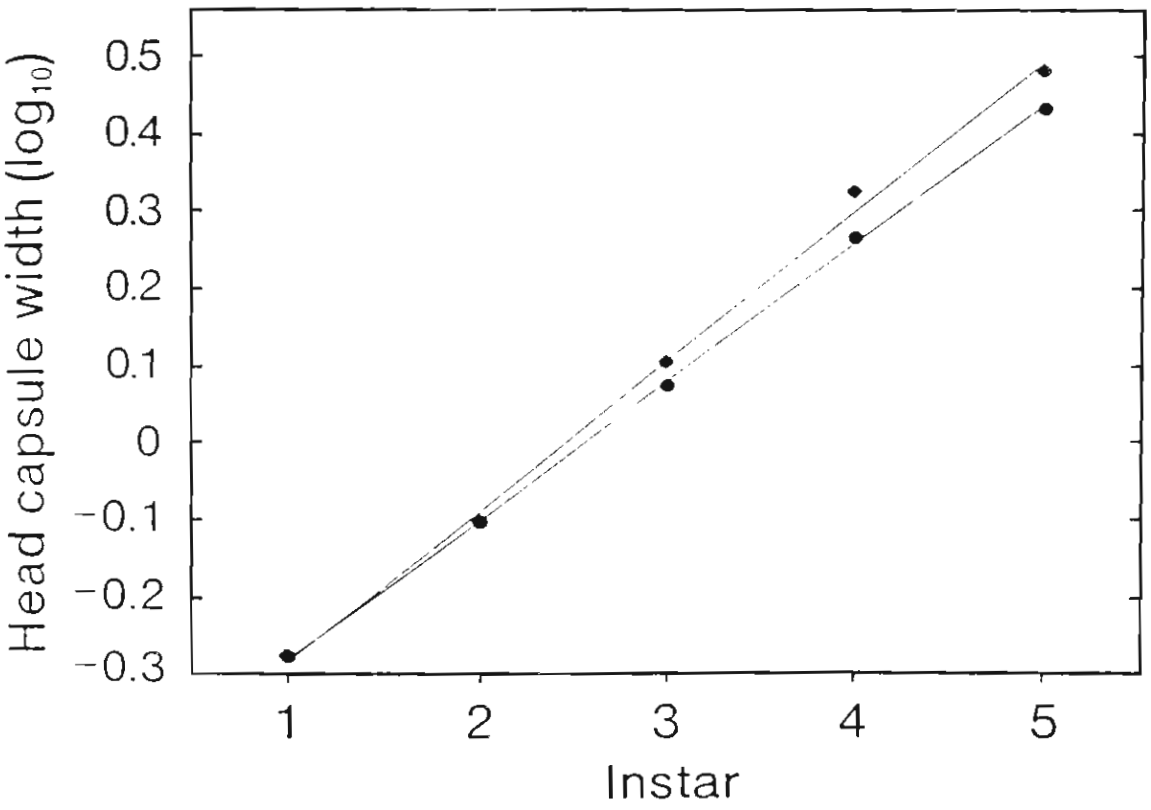
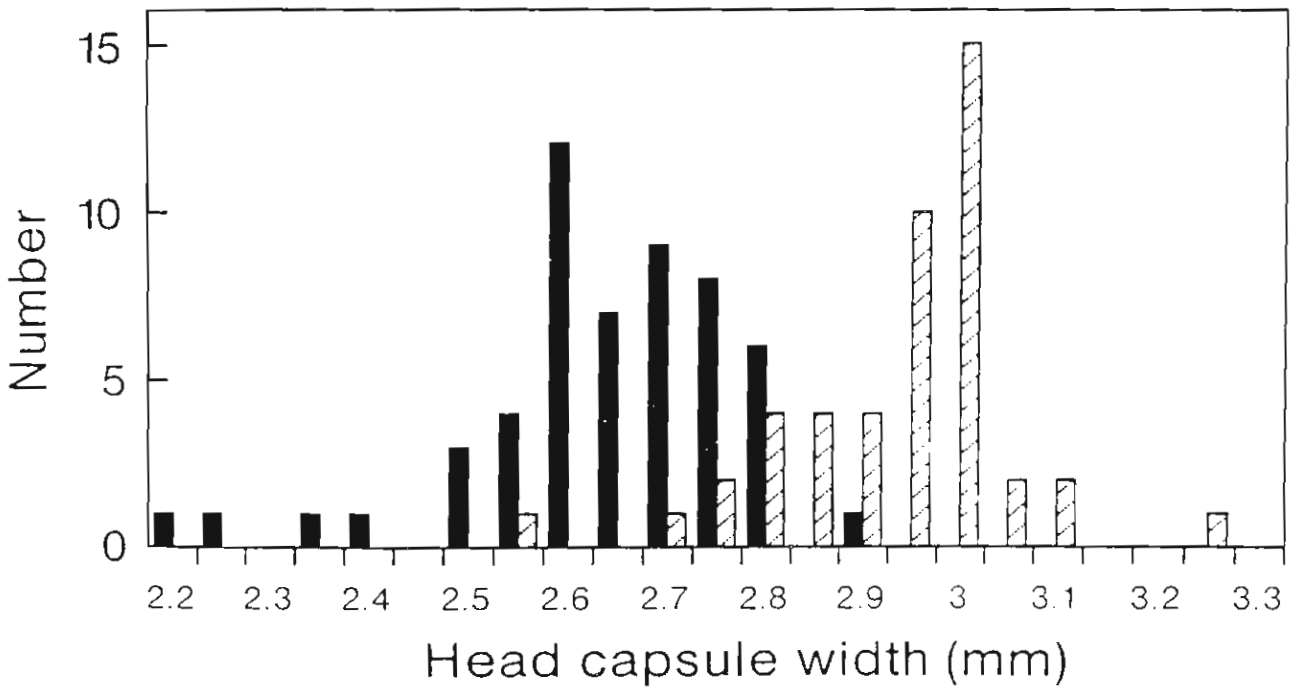
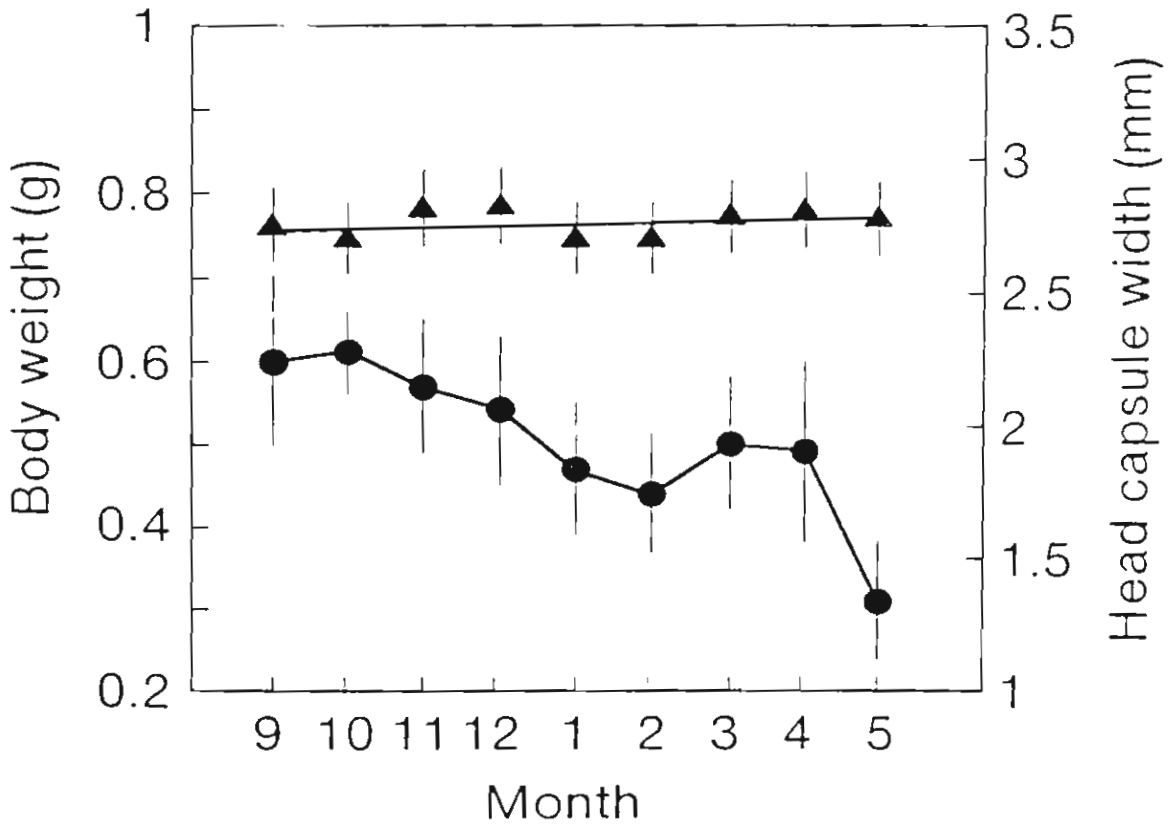

0.6
0.4
0.2
0
-0.2
-0.4
Head capsule width (log_{10})
1
2
3
4
5
Instar

Figure 6




15
10
5
0
Number
2.2
2.3
2.4
2.5
2.6
2.7
2.8
2.9
3
3.1
3.2
3.3
Head capsule width (mm)


Body weight (g)
1
0.8
0.6
0.4
0.2
Head capsule width (mm)
3.5
3
2.5
2
1.5
1
9 10 11 12 1 2 3 4 5
Month

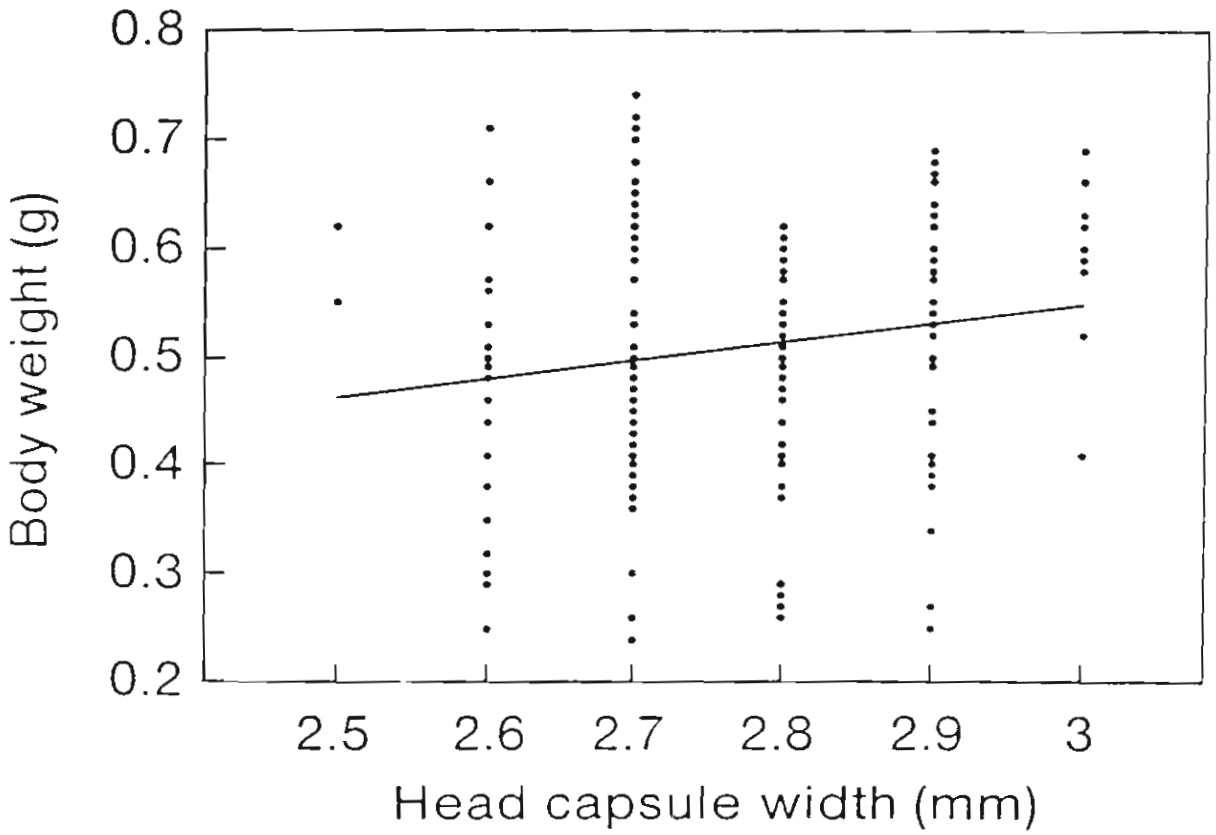
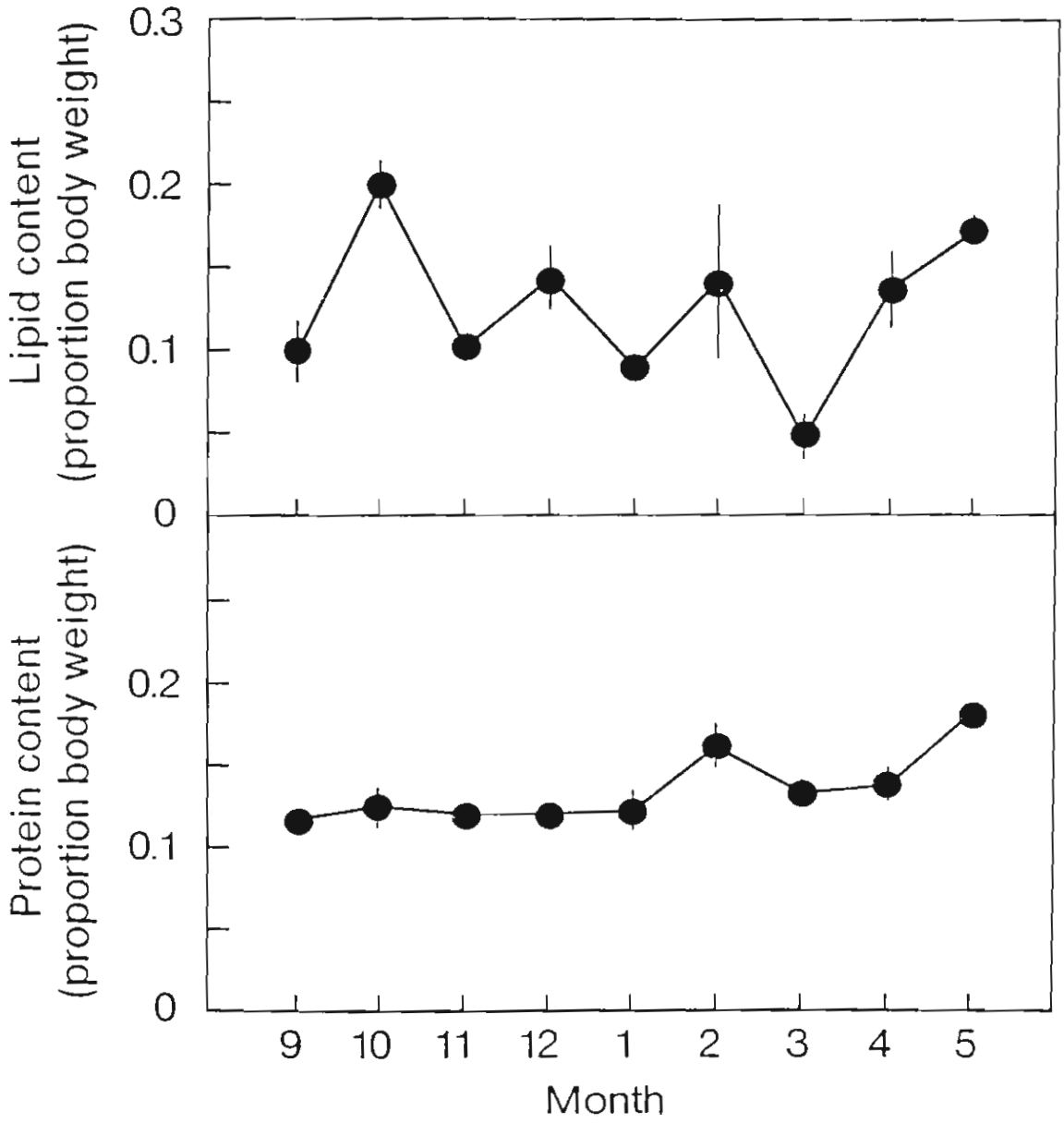
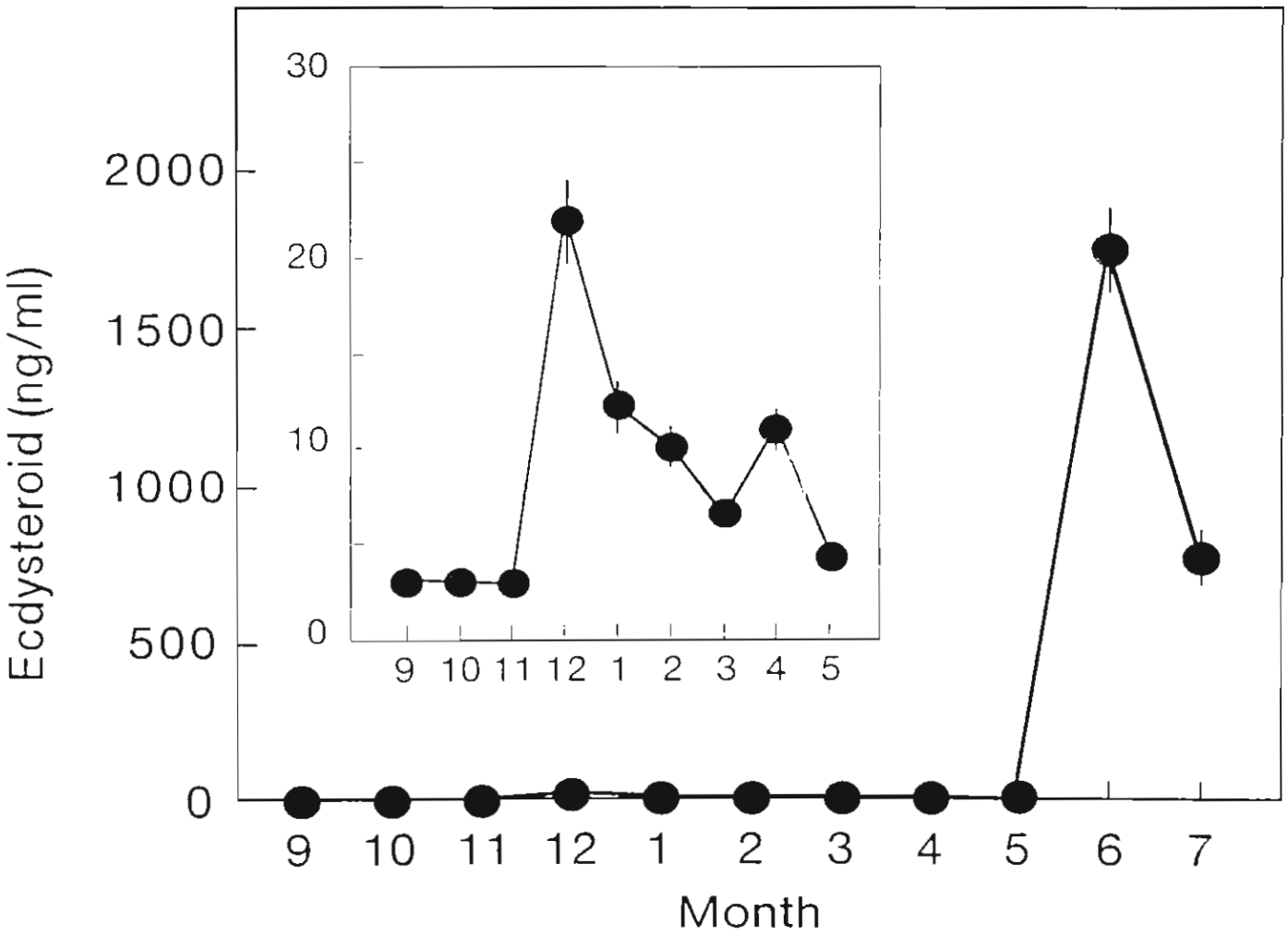

0.8
0.7
0.6
0.5
0.4
0.3
0.2
Body weight (g)
2.5
2.6
2.7
2.8
2.9
3
Head capsule width (mm)

Figure 10


Lipid content
(proportion body weight)
0.3
0.2
0.1
0
Protein content
(proportion body weight)
0.2
0.1
0
9
10
11
12
1
2
3
4
5
Month


Ecdysteroid (ng/ml)
2000
1500
1000
500
0
9 10 11 12 1 2 3 4 5 6 7
Month
30
20
10
0
9 10 11 12 1 2 3 4 5