INSTAR SIZES AND GROWTH IN THE MIDDLE PERMIAN MONURAN *DASYLEPTUS BRONGNIARTI* (INSECTA: MACHILIDA: DASYLEPTIDAE)

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Abstract—We used probability plotting to identify six sequential instars in the monuran *Dasyleptus brongniarti* Sharov, 1957. Data from 25 specimens from the Middle Permian (Ufimian) Kaltan locality in the Kuznetsk Formation in southwestern Siberia were used in the study. A probability plot of the statistical distribution of body lengths (excluding the caudal filament) shows six distinct normal component modes that represent size groups. The most parsimonious explanation of the size groups is that they represent instars. The component modes were resolved to yield the approximate mean size and standard deviation for each instar. These resolved instar data were then used to generate a partial growth curve that spans the range of 3.5 to 12 mm.

The resolved instars of *D. brongniarti* compare favorably to those of the extant wingless insects, the silverfish, *Lepisma saccharinum*, and the bristletail, *Petrobius*. Using *L. saccharinum* as a model, the *D. brongniarti* instars probably represent numbers five through 10. The instar sizes generally obey Przibram's rule, which predicts a doubling of mass and hence an increase of (factor of 1.26) in the linear dimensions at each molting. Our *D. brongniarti* data show body length increasing by a factor that varies between 1.13 and 1.37 at each instar, and averaging 1.24 over the six instars.

MATERIALS AND METHODS

The Monura are primitive wingless insects known as fossils from the Pennsylvanian and Permian strata (Tasch, 1973). They are united with their extant relatives the bristletails and silverfish by several characters: all are wingless, similar in size and form, have well developed antennae, ununited thoracic segments, and molt throughout their lifetimes (Carpenter, 1992).

Rasnitsyn (1999) redescribed the monuran *Dasyleptus brongniarti* (Fig. 1) and assembled a morphometric database of 25 specimens of the species. All the specimens are from the Kaltan locality in the Kuznetsk Formation of southwestern Siberia and are currently located at the Paleontological Institute, Russian Academy of Sciences, Moscow, Russia. The Kuznetsk Formation is Middle Permian (Ufimian) in age (Zhuravlev and Ilynia, 1988). Body lengths (excluding the caudal filament) of the 25 specimens are shown in Table 1. With this relatively large database, it was possible to use a statistical method to investigate their growth characteristics. Thirty or more specimens would have been the preferred statistical sample size, but 25 specimens yielded a satisfactory result. We applied a probability plotting method to the body length data of these specimens to test for statistical size groupings that could represent life stages between moltings (instars).

A very brief explanation of the probability plotting method is included here. It is by no means comprehensive and only attempts to elaborate on the specifics pertinent to interpreting the *D. brongniarti* data. Probability plotting is a simple, powerful, graphic method of comparing a data set to a statistical distribution function. A probability plot shows the probability (x axis) that a random observed variable will be less than or equal to a given value (y axis). Probability calculations are simple and the plots are easily made by hand, but here we used KaleidaGraph (1997) graphic analysis software to produce publication quality output. The probability data are plotted against a scale that is generated by a specific distribution function (e.g., normal, log normal, extreme, etc.). Straight line fits of the data to a specific probability scale indicate that the data are distributed according to the function used to generate that scale. Departures from a straight line fit indicate that the data are skewed, truncated, multi-modal, or do not fit the distribution function (King, 1971; Kock and Link, 1970).

A normal (Gaussian) probability plot (Fig. 2A) of *D. brongniarti* body lengths has several "plateaus" that vary from horizontal to some-
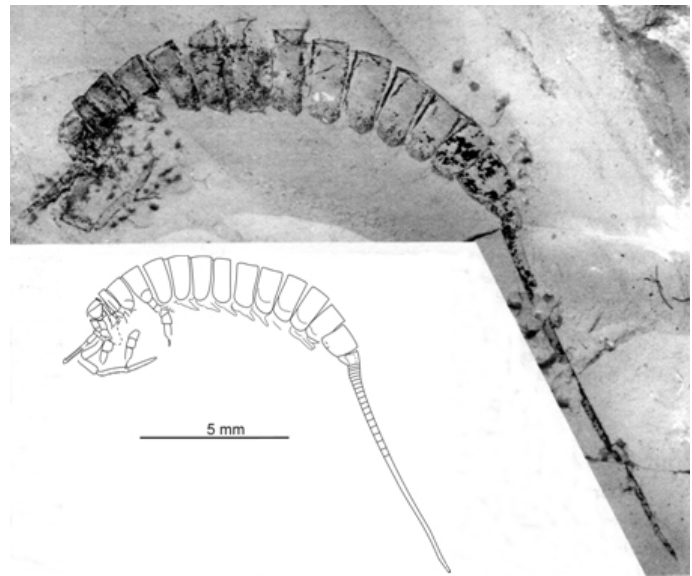

FIGURE 1. The holotype of *Dasyleptus brongniarti* Sharov, 1957. Photo from Carpenter (1992, figure 11B), and reconstruction from Rasnitsyn (1999) figure 6 (based on the holotype plus several paratypes).

what inclined. These indicate that the overall distribution of body lengths comprises several component modes (King, 1971). A smooth curve drawn through the data points shows that the plateaus are connected by steep jogs that contain concave-up to concave-down inflections (proceeding left to right). These inflection points indicate the approximate "boundaries" of the component distributions (Knoop and Owen, 1994; Peck, 1987). Theoretically, the distributions expand infinitely in either direction from the mean, but given a finite data set, the inflection points provide a very good approximation of the limits of each component mode. Only the concave-up to concave-down inflections are used to show the component mode boundaries; concave-down to concave-up inflections indicate the approximate mean of the components. We separate the overall distribution (Fig. 2A) into its six components at the inflection points (X's in the figure) and replot each component (Fig.

FIGURE 3. Growth in *D. brongniarti*; a step plot of six resolved instars (solid line) with ±s (dotted lines). Approximate instar numbers are based on comparison to those of the silverfish, *Lepisma saccarinum*.

2B). The straight line curve-fits to the components indicate that they have been correctly resolved and that they are normal (Peck, 1988). The uppermost component contains only two members and is, of course, a very rough approximation.

The mean value and standard deviation (s) of each component may be read directly off the plot. The mean value occurs at the 50% probability point; +s and -s occur at the 84% and 16% probability points respectively (King, 1971). For greater accuracy, we used the coefficients of the linear curve fits (Fig. 2B) provided by the graphic analysis software. Mean values and standard deviations of the resolved instars are given in Table 2.

DISCUSSION

The mean values of the resolved instar sizes were used to generate a step plot (Fig. 3), which is a partial growth curve for *D. brongniarti*. The approximate instar numbers are assigned based on the similar-sized modern silverfish *Lepisma saccarinum* (Zygentoma: Lepismatidae) which is ~ 4.1 mm long in its fifth instar (Delaney, 1957) and attains an adult length of 15 to 20 mm. *L. saccarinum* has 11 to 13 pre-breeding instars (Sharov, 1953) and continues ecdysis as an adult, molting as many as 35 times in its 45 month lifetime (Larink, 1983). The resolved instars of *D. brongniarti* also fall within the range of the modern bristle-tail, *Petrobius* (Archaeognatha: Machilidae), which has seven to eight pre-breeding instars (Smith and Watson, 1991). The number of instars in *D. brongniarti* is unknown and may or may not exactly match those of *Lepisma*, nonetheless, a substantial segment of the pre-breeding growth curve of the animal has been reconstructed. The span of the retrieved growth curve is 3.5 to 12 mm and represents most of the
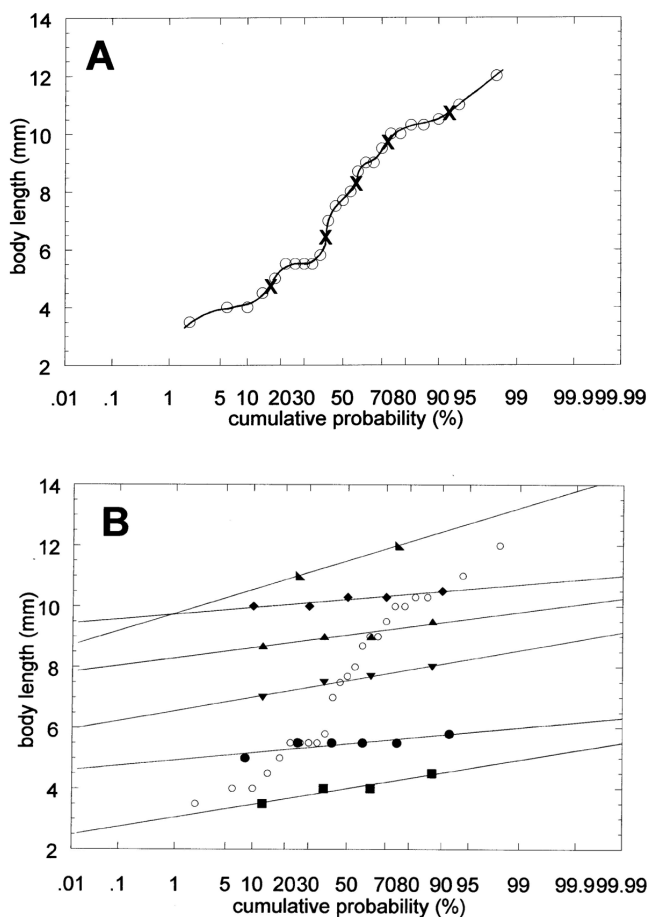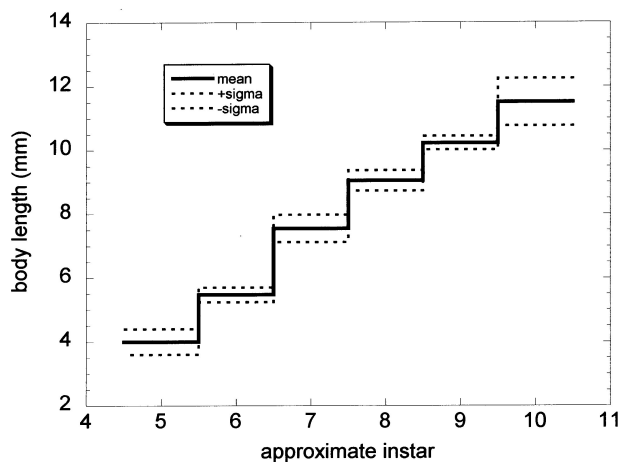
FIGURE 2. A: A normal (Gaussian) probability plot of body lengths of 25 specimens of *D. brongniarti* showing multi-modal behavior. A smooth curve is drawn through the data points (open circles) and the concave-up to concave-down inflection points are indicated by X's. B: A normal probability plot of the original multi-modal distribution (small open circles) plus the six resolved component modes (filled symbols) with linear curve fits.

TABLE 1. Body length of 25 specimens of *D. brongniarti* used in the analysis.

specimen	body length (mm)	specimen	body length (mm)
1197/595 (holotype)	10.3	1197/594	12
679/75	~5	1197/596	5.5
966/14	10.3	1197/597	~4
966/15	9	1197/598	9.5
966/16	~10	1197/601	~9
966/17	~4.5	1197/602	8
966/18	~10.5	1197/603	8.7
966/19	~10	1197/605	~4
966/20	~5.5	1197/608	5.8
1197/585	~11	1197/609	~5.5
1197/586	~7.5	1197/610	~3.5
1197/587	~7	1424/4	~5.5
1197/592	~7.7		

TABLE 2. Mean body length, standard deviation, and growth factor of the resolved instars of *D. brongniarti*.

resolved instar	mean value (mm)	standard deviation (mm)	growth factor
A	4.0	0.40	
B	5.47	0.23	1.37
C	7.55	0.43	1.38
D	9.05	0.32	1.2
E	10.22	0.21	1.13
F	~11.5	~0.74	1.13
average growth factor		1.24	

prebreeding size range of *D. brongniarti.*

Our *D. brongniarti* growth data closely follow Przibram's rule. This empirical rule is based on the idea that insect larvae roughly double their number of cells and hence their mass between molts. Since mass is proportional to the cube of the linear dimensions, the dimensions should increase by or a factor of 1.26 at each instar (Wigglesworth, 1972). Although many exceptions to Przibram's rule may be noted, it does have value as a *first rough approximation* (Thompson, 1942). We show the growth factor by which the body length of *D. brongniarti* increases at each of the resolved instars (Table 2). This factor is gener-

ated by dividing the body length of each instar by that of the previous instar; (N+1)/N, where N is the instar number. The body length increase per instar varies from 1.13 to 1.38, and averages 1.24 over the six instars.

We have shown that growth in the monuran *D. brongniarti* follows the same pattern as is seen in its extant relatives. It would thus be assumed, not surprisingly, that the same growth mechanisms and regulating principals were already in operation in these Middle Permian animals.

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