

# A MORPHOLOGICAL STUDY OF LARVAL DEVELOPMENT IN POLYMORPHIC ALL-WORKER BROODS OF THE ARMY ANT *ECITON BURCHELLI* (1, 2)

by

Eleanor Rita LAPPANO (3)

(The American Museum of Natural History and Fordham University.)

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(3) Present address: Fourth Surgical Division, New York University, Post-Graduate Medical School, New York 16, New York.

## INTRODUCTION

The social behavior of the army ants *Eciton burchelli* and *Eciton hamatum* characterized by alternating, cyclic phases of nomadic and statary activity, is directly dependent upon and synchronized with the development and reproduction of successive all-worker broods appearing at regular intervals (SCHNEIRLA, 1938, 1944 a, 1944 b and 1949). Schneirla's studies show that the larval stage of development of these holometabolous insects occurs in the nomadic phase of activity, and that this phase ends when the mature larvae spin cocoons. In the statary phase which follows, this same developing brood, now enclosed in cocoons, undergoes its pupal period of metamorphosis. Midway through each statary phase, the single queen of each *Eciton* colony lays many thousands of eggs over a period of about six days (SCHNEIRLA, 1953 a). Hence, the embryonic and early larval development of the next brood of ants occurs at the same time that the previous brood is undergoing late pupal development. The statary phase ends when the new adults (or callows) emerge from their cocoons, thus initiating another nomadic phase of activity.

This intricately synchronized life cycle, and its complex behavioral aberrations, continues throughout the year, resulting in the production of polymorphic, all-worker populations ranging near 120,000 individuals every thirty-six days in *burchelli*, and about half as many in *hamatum*. Once a year, at the onset of the dry season, a sexual brood of approximately 1,500 males and about six queen-type females are produced (SCHNEIRLA, 1953 a).

Until SCHNEIRLA's studies, little of the present evidence on the behavior pattern and nothing of the life cycle of these interesting ants were known. Through his work, preserved specimens of their various developmental stages first became available for study, for along with observations on colony behavior of all colonies studied in the field, SCHNEIRLA collected and preserved samples of the adult and developing brood populations. These samples were made available for the present morphological investigations of *Eciton burchelli* and *Eciton hamatum* development.

A review of the literature shows that previous studies of *E. burchelli* all-worker brood development are lacking. Even the most general descriptions of the external morphology of the larvae at any stage are scarce and incomplete. The worker larvae of *E. burchelli* were first described by EMERY (1899 and 1901) and G. C. WHEELER (1943) has added further details to this description. The external morphology of *E. hamatum* worker larvae was described in a preliminary manner by G. C. WHEELER (1938 and 1943) and a more detailed account of this form is reported by TAFURI (1951). Using specimens collected by SCHNEIRLA, TAFURI investigated the developmental morphology of *hamatum* worker larvae with an account of the growth of these polymorphic forms expressed as a ratio of body length to imaginal leg-disc size at successive stages. Also a description of some of the internal anatomy of *hamatum* larvae throughout development is given.

The present investigation was undertaken to study the external and internal morphology of *E. burchelli* throughout most of the stages of larval development to its conclusion, and to determine whether differences in developmental growth rate and in structure exist among the various polymorphic forms of the larval brood. It was found that in the various polymorphic size-groups of *burchelli* larva there are differences in the size and growth rate of the imaginal leg discs throughout development, as well as differences in terms of the 'phase-day' age at which developmental changes in the leg discs and in the labial or spinning glands occur. The times at which such changes are first observed in larvae of the different polymorphic size-groups are correlated with changes in colony behavior and function reported from field studies on this species, and appear to depend upon certain factors underlying differential growth and development of these ants. The present paper is therefore devoted to the description of the external and internal anatomy of *Eciton burchelli* larvae, with emphasis on the developmental morphology of the leg discs and the labial glands.

## MATERIALS AND METHODS

**THE BROOD SAMPLES.**—The *E. burchelli* larvae studied were from the collections of colony samples of the American Museum of Natural History. These samples were collected and preserved by T. C. SCHNEIRLA and R. Z. BROWN on Barro Colorado Island, Canal Zone, Panama, during various field expeditions. The age of the larvae was initially designated upon the basis of specific characteristics noted in colony behavior at the time of collections. All larvae were fixed in Bouin's fixative or 95 per cent alcohol at the time of collection and then stored in 70 per cent alcohol containing two per cent glycerine.

Each day's sample consists of all individuals captured from an all-worker larval brood and preserved on a given day of the statary or nomadic phase. The samples were collected by a procedure intended to give the best obtainable representation of the polymorphic brood range. Because the bivouacs of *burchelli* colonies are at times unapproachable for the collection of any brood sample at all, or may be so situated in the bivouac that the collection of the brood sample is limited to one part of the polymorphic range, no colony in this study is represented by samples at regular intervals throughout development. Therefore, the broad interval from late embryonic to mature larval development had to be represented by samples from different colonies, and thus forms a 'synthetic series' of all-worker *burchelli* brood development. The samples studied, which collectively represent *burchelli* brood development were: '52 B-I, last statary day; '47 B-II, third, eighth and tenth nomadic days; '46 B-IV, fifth and seventh nomadic days; and '46 B-I, twelfth nomadic day. Additional studies of *burchelli* larvae were carried out on samples of '53 B-II, third nomadic day; '53 B-I, ninth nomadic day; and '46 B-I, last nomadic day.

Each colony number designates the particular colony on which detailed field observations of colony behavior were made by SCHNEIRLA (SCHNEIRLA, 1949, and SCHNEIRLA and BROWN, 1952). For example, '46 B-IV signifies the fourth *E. burchelli* colony studied in 1946.

Since at each successive time throughout the activity cycle of the terrestrial Ecitons, characteristic changes are noted in the developmental condition of the brood (SCHNEIRLA, 1934, 1944 b and 1953 a; SCHNEIRLA and BROWN, 1950), each further day's sample may be considered to represent an advance in development. This correspondence has been found to hold in all colonies. However, in the present study of the synthetic series assembled from different colonies for the study of all-worker brood development of *burchelli*, secondary variants appear which may modify, to a limited extent, the relationship of the 'phase-day' age to the developmental stage which would be expected in the brood of a single colony. These may be the results not only of limited inter-colony differences, but also of deviations in the intervals due to the impossibility of collecting the samples at the same time of day.

**SELECTION OF SPECIMENS IN THE POLYMORPHIC RANGE.**—The number of *burchelli* larvae in each day's sample varied from approximately 150 to 3,000-4,000, with the usual number about 300-400. To insure a study of the complete range of polymorphic larval forms present in each sample, eight of the largest specimens, eight of the smallest and 24 of sizes graded between the extremes were selected to represent each sample. A dissecting microscope was used in selecting specimens of the early developmental stages. Half of these larvae (four large, four small and twelve of graded sizes) thus taken from each day's sample were measured in detail and a study was made of their external and internal morphology. The remaining 20 were used for dissections and for whole mount preparations.

**STUDY OF EXTERNAL AND INTERNAL MORPHOLOGY.**—The *burchelli* larvae selected for study of their external morphology were examined under a dissection microscope and the following data were recorded: The shape of the larva and its state of preservation; the condition of the cuticle; the presence, quantity and distribution of cuticular hairs; the transparency of the cuticle; the presence and extent of development of the imaginal

leg discs (their size, shape, segmentation and position with respect to the margin of their segment); and the presence and state of development of the antennal discs, the gonopodal discs and the mouth parts. Measurements were taken of the total body length and width and the dimensions of various segments, also the length and width of one randomly selected left or right leg disc of each of the three pairs.

All of the measurements were made with a filar micrometer except in the case of total body length, for which an ocular micrometer was used.

For study of the internal morphology of *burchelli* larvae the specimens were dehydrated and imbedded in paraffin using the normal butyl alcohol method (LEE, 1937). Sections were cut at six micra and stained with either Heidenhain's iron alum haematoxylin or Harris' standard haematoxylin counterstained with eosin (GALIGHER, 1934). Whole mounts of the larvae, and of dissected organs, were prepared using Lynch's precipitated borax-carmin technique (GALIGHER, 1934).

## RESULTS

### EXTERNAL MORPHOLOGY

*General inspection of the polymorphic larval range.*—It is apparent from the results of this study that the larvae in the sample of any one day are not synchronized linearly, and that they must differ either in the time at which their respective larval developments were initiated, in the rate of their development, or in both of these. This impression is soon borne out by the results of general body measurements as of length in relation to specific measurements of body parts such as leg discs (table 1).

First, an inspection of the brood sample collected at any one time reveals a wide range in body length with indications of individual differences in detailed morphology possibly bearing a different relationship to overall body size in the respective parts of the range. That this must be the case becomes evident when individual differences in the degree of development of detailed larval structures such as the leg discs, mouth parts, cuticular hairs and the gonopodal discs are taken into account. The general picture indicated is one in which, at any one cross-section in time, a smooth gradation is found from specimens of maximal to those of minimal body length, with differences in the time of appearance, size, and degree of development of structural details relative to differences in overall size.

Furthermore, when specimens from samples collected at successive different times are compared, it is apparent that overall size cannot be a reliable clue to developmental stage, unless the relationship between body size and the condition of the details of structures is taken into account.

*The largest larvae or potential workers major.*—The largest larval specimens, apparently the potential workers major, evidently develop from the first eggs to hatch and thus obtain a precocious growth advantage over the smaller members which hatch from their eggs in the late statary

AGE	GROUP**	BODY LENGTH IN mm.			AREA LEG DISCS IN mm <sup>2</sup>			RATIO IN LOG 10 <sup>-4</sup>
		RANGE			RANGE			
		MINIMUM	MAXIMUM	AVERAGE	MINIMUM	MAXIMUM	AVERAGE	
LAST STATARY DAY	S	0.504	0.604	0.513	.000	.000	.000	0
	G	0.717	2.076	1.248	.000	.000	.000	0
	L	2.604	2.982	2.651	.004	.006	.005	1.276
3rd NOMADIC DAY	S	0.520	0.569	0.548	.000	.000	.000	0
	G	0.604	3.434	1.544	.000	.008	.001	0.811
	L	4.189	5.887	4.651	.001	.013	.008	1.236
5th NOMADIC DAY	S	1.510	1.698	1.528	.000	.003	.000	0
	G	1.736	5.623	3.658	.000	.020	.005	1.135
	L	5.623	7.322	6.095	.011	.030	.011	1.255
7th NOMADIC DAY	S	1.925	4.604	3.201	.000	.012	.000	0
	G	4.944	7.472	6.091	.000	.037	.006	0.993
	L	7.661	8.739	7.557	.000	.019	.003	0.598
8th NOMADIC DAY	S	0.906	1.547	1.246	.000	.000	.000	0
	G	2.717	6.302	4.013	.000	.022	.010	1.396
	L	6.680	9.107	7.086	.000	.029	.022	1.492
10th NOMADIC DAY	S	2.076	3.107	2.726	.000	.007	.001	0.564
	G	3.623	7.548	5.642	.000	.054	.023	1.610
	L	8.152	10.000	8.095	.000	.066	.038	1.666
11th NOMADIC DAY	S	4.416	5.170	4.838	.012	.016	.013	1.429
	G	5.812	8.000	6.391	.016	.048	.027	1.626
	L	9.095	10.492	9.086	.013	.049	.032	1.547
12th NOMADIC DAY	S	3.700	4.868	4.112	.009	.022	.017	1.616
	G	5.170	9.360	6.866	.000	.050	.024	1.543
	L	9.624	13.800	11.405	.000	.088	.022	1.285

\* The four smallest individuals are grouped under letter S, the four largest individuals are grouped under letter L, and the twelve individuals of graded sizes are grouped under letter G.

\*\* The ratio here listed was obtained by dividing the average leg discs' area by the average body length.

TABLE 1. — Measurements of *Eciton burcheelli* larvae throughout development.

or early nomadic phase. This precocious growth advantage is maintained throughout the entire larval stage of development. Thus, in samples taken at the earliest larval stages, prominent morphological features such as the earliest stages of development of the mouth parts, the imaginal leg discs, the antennal and gonopodal discs and the cuticular hairs are observed in the specimens having the greatest body length and width, but not in the smallest larvae. It should be noted then that there are two methods of calibrating developmental progress: First, by using the nomadic day, that is, specimen staken from day one to day thirteen, each day denoting the development in termes of the representative duration of time. A second method of calibrating developmental progress makes use of the developmental stage. Here the different polymorphic types are considered roughly comparable in the time at which hatching occurs, in the representative times thereafter in which corresponding changes appear in structure (e.g., leg discs), and in the respective times at which they attain larval maturity. In general,

as table 2 shows, these corresponding changes appear first in the largest larvae, next in the larvae of intermediate sizes and last in the smallest larvae.

TIME OF APPEARANCE OF DEVELOPMENTAL CHARACTERISTICS OF AN ALL-WORKER  
LARVAL BROOD OF ECITON BURCHELLI

LARVAL SIZE	LARGEST (POTENTIAL WORKER MAJORS)	INTERMEDIATE (POTENTIAL WORKER INTERMEDIATES)	SMALLEST (POTENTIAL WORKER MINIMAS)
EXTERNAL DEVELOPMENT			
	TIME OF FIRST APPEARANCE		
EMBRYONIC DEVELOPMENT	MIDDLE TO LATE STATARY PHASE	LATE STATARY PHASE	VERY EARLY NOMADIC PHASE.
CUTICULAR HAIR DEVELOPMENT	LAST STATARY DAY	3 <sup>RD</sup> TO 5 <sup>TH</sup> NOMADIC DAYS	7 <sup>TH</sup> NOMADIC DAY.
MOUTH PARTS DEVELOPMENT	LAST STATARY AND FIRST NOMADIC DAYS.	5 <sup>TH</sup> TO 7 <sup>TH</sup> NOMADIC DAYS	11 <sup>TH</sup> TO 13 <sup>TH</sup> NOMADIC DAYS
IMAGINAL LEG-DISC DEVELOPMENT	LAST STATARY DAY	3 <sup>RD</sup> TO 7 <sup>TH</sup> NOMADIC DAYS.	8 <sup>TH</sup> TO 9 <sup>TH</sup> NOMADIC DAYS.
INTERNAL DEVELOPMENT			
	FUNCTIONAL ONSET OF SALIVARY SECRETION		
BASOPHILIC PROLIFERATION OF GLANDULAR PORTION.	LAST STATARY AND FIRST NOMADIC DAYS.	3 <sup>RD</sup> NOMADIC DAY	MAINLY BY 6 <sup>TH</sup> NOMADIC DAY.
LABIAL PORTION DENSE CYTOPLASM, AND IRREGULARITY OF CUBOIDAL CELLS.	8 <sup>TH</sup> NOMADIC DAY.	9 <sup>TH</sup> NOMADIC DAY	10 <sup>TH</sup> NOMADIC DAY
ANTERIOR DUCT AND GLANDULAR PORTIONS DISINTEGRATING.	10 <sup>TH</sup> NOMADIC DAY	11 <sup>TH</sup> NOMADIC DAY	12 <sup>TH</sup> AND LAST NOMADIC DAYS
ACCUMULATION OF ACIDOPHILIC MATERIAL IN LUMEN	10 <sup>TH</sup> NOMADIC DAY	12 <sup>TH</sup> AND LAST NOMADIC DAYS	13 <sup>TH</sup> NOMADIC DAY

TABLE 2. — The times of first appearance and of the apparent onset of function of various external and internal structures and various organs characteristic throughout development in all-worker larval broods of *Eciton burchelli*.

A precocious growth in the largest larvae is indicated by the fact that in the material studied, the largest members of the sample taken at the tenth nomadic day may be considered fully mature and ready to enter the prepupal period of metamorphosis at a time when smaller members of the range are relatively less mature. At this time these larvae approximate a cylindrical shape with their narrow anterior ends curved ventrally (fig. 1). The body widens posteriorly to the region of the fourth or fifth abdominal segment, where it begins to taper and finally terminates bluntly at the posterior end. All of the larvae have fourteen segments,—a head segment, three thoracic segments and ten abdominal segments. The last abdominal segment is usually small and not as distinct as the other thirteen.

**Structural indications of development.**

**A. Shape and body curvature.** — During embryonic and early larval development, the head segment is the largest segment of the body, but by the time the larvae reach a length of approximately one millimeter, the

thoracic segments have become the largest segments, and the widest part of the larvae is in the abdominal region.

In preserved larvae representing very early stages (e.g., the last statary and the third nomadic days) the largest larvae show little ventral curvature in their anterior segments, in contrast to the considerable curvature noted in mature specimens (e.g., the largest larvae of the tenth nomadic day and the intermediate specimens of the last nomadic day). It therefore appears that a direct relationship exists between the amount of body curvature and body length in the preserved material. In all the polymorphic forms, just before maturity, the larger the larva the greater the amount of curvature.

**B. Cuticle.**—Although in most of the *burchelli* larvae studied the cuticle was characteristically papillose as described by G. C. WHEELER (1943), a relatively smooth cuticle was observed in many instances. This is probably related to the occurrence of moulting, for when a double cuticle is seen its inner cuticle is invariably papillose, whereas the outer cuticle is usually smooth. In the mature larva the cuticle is opaque in all segments except the head segment where it is slightly transparent, whereas in younger and smaller larvae the cuticle is very transparent so that the nerve cord, digestive tract and other internal organs can be seen through it. As development proceeds, the cuticle becomes opaque and may take on a chalky appearance in various regions.

Study of the appearance of cuticular hairs on the different regions of larvae in the successive samples, and the progressive development of the hirsute covering, revealed that at early stages (e.g., in larvae of the last statary day) the cuticle possesses hairs only in the largest larvae, (e.g., longer than 3.4 mm) and is smooth in larvae of the smaller sizes. This condition persists, substantially as described, in more advanced samples taken on the 3rd., 5th. and 7th. nomadic days. A relative change, i.e., appearance of a hirsute cuticular condition in the smaller castes, is indicated by the fact that minute, bristle-like hairs are present on the head and thorax of the 3.5 to 5.8 mm larvae of the third nomadic day and on the 3.4 to 5.0 mm larvae of the fifth nomadic day. Numerous short, simple hairs are present on the head, thorax and posterior end of the abdomen in the 5.7 to 7.3 mm larvae of the fifth nomadic day, and on all larvae greater than 3.4 mm of the seventh nomadic day. The largest larvae of the seventh nomadic day, and successively smaller individuals of further nomadic days, have progressively more hairs on their thorax and abdomen, another indication that hirsuteness varies in relation to body length and age. In samples taken at the tenth nomadic day, when the largest larvae have reached maturity, all the larvae throughout the range from smallest to largest are covered with numerous hairs quite evenly distributed over the surface of the body.

**C. Mouth parts.**—In the mature larvae, the mouth parts are the dorsally situated fleshy labrum, the dorso-lateral heavily sclerotized, sickle-shaped

mandibles, the large fleshy laterally arranged maxillae, and the ventral labium (figs. 2 and 3). The maxillae possess two pairs of palps; the conically-shaped, sclerotized galea, and the more posteriorly situated maxillary palps (fig. 2). The latter, are broad, roughly ridged and sclerotized. On the anterior surface of the labium, and slightly elevated, is the horizontal, slit-like opening of the labial glands, or sericteries. Just lateral to this opening are the minute, conically-shaped, slightly sclerotized labial palps (figs. 2 and 3).

This description of the mouth parts agrees with the previously reported mouth parts for the larva of *E. burchelli* (EMERY, 1899 and 1901, and G. C. WHEELER, 1943).

The labrum, mandibles, maxillae and labium appear first in the largest (.604 mm) larvae at earliest stages (last statary and third nomadic days), and in all larger and older samples they are found throughout the size range. Throughout the nomadic phase of development the mandibles are heavily sclerotized in larvae of all sizes. The galea and maxillary palps, in contrast, first appear and subsequently become sclerotized at a different time, a fact which is found to serve as an index to larval maturity.

The galea and maxillary palps also develop precociously in the largest larvae, as is indicated by the fact that their most sclerotized condition is observed first in the largest larvae of each successive sample. In the sample of the thirteenth day, in which distinct signs of maturity are noted throughout the larval brood, even the smallest larvae exhibit an advanced degree of development in these structures. Of course, at all stages these structures, and others as well, exhibit size variations related to overall body size.

These studies indicate a developmental precocity which is greatest in the largest larvae, very probably the potential workers major, and least in the smallest larvae, or potential workers minima. However, there are indications that although the smallest larvae are last to complete the initial period of slower overall developmental acceleration, in their case the rate of development of these structures is subsequently greater than in the larger larvae (intermediate and major castes). This point may be better examined with respect to the imaginal leg discs, which make their first appearance at different times and undergo their subsequent growth at a different rate in larvae of the three size groups selected for study.

**D. Imaginal leg discs.**—G. C. WHEELER (1938), in describing the vestigial legs of the army ant larva, has referred to the relevant imaginal discs. These are three pairs of round or oval patches of hypodermis located on the ventral surface of the thoracic segments (fig. 4). The first appearance and progressive enlargement of the imaginal leg discs occur at a different time and at a different rate in larvae of each of the three polymorphic size groups. In our earliest samples (i.e., from the last statary and first nomadic days) the discs are found only in the largest larvae; in subsequent samples they are found successively later in the



intermediate and the smallest larvae. The leg discs were not found in the smallest or minim larvae before the sample of the seventh nomadic day.

E. **Differential growth rate of the leg discs.**—As the imaginal leg discs represent our indicator of local growth in the more detailed study of development in *Eciton burchelli* larvae, it is appropriate here to describe in further detail how the obtained measurements were treated. First, one randomly selected member of each pair of imaginal leg discs was measured in its length and width in each specimen of the four largest, four smallest, and twelve larvae of intervening sizes in each sample, with each of the larvae also measured in its overall body length. Then a theoretical expression was obtained for leg disc status in each larva by first obtaining the *length*  $\times$  *width* product for each of the three discs measured, then averaging, the three products for each individual. These results are listed in Table 4, as three groups of averages of the larval leg-disc areas for each developmental stage studied, together with the similarly averaged ratios obtained by calculating *body length* : *leg-disc area*. This ratio of body length to the leg-disc area value serves as an expression of allometric growth status for larvae in samples taken at different stages of development.

With very few exceptions, primary developmental stages of the imaginal leg discs are present in *burchelli* larvae with body length greater than 2.6 mm of the last statary day; 2.4 mm of the third nomadic day; 2.3 mm of the fifth nomadic day; 2.0 mm of the seventh nomadic day; 2.7 mm of the eighth; 2.9 mm of the tenth and in all individuals of successive nomadic days. Hence there appears to be a relationship between the onset of leg-disc development and the attainment of a given threshold of size in the larva rather than to the phase-day age of the larvae. This is evident when one considers the fact that leg discs appear at correspondingly later phase-day ages in those larvae lest to hatch and to begin their development (i.e., in the smallest or potential minim castes).

In all samples, the leg discs exhibit their most advanced stages in the largest larvae. Thus in the sample of the third nomadic day, the presence of the peripodal cavity is apparent in some of the largest larvae but in none of the smaller specimens. In like manner, in the sample of the fifth nomadic day the presence of transverse segmentation in these discs is apparent in some of the largest larvae but not in any of the smaller specimens. These changes in the development of the leg discs are always observed first in the largest larvae, only later in the intermediate (size-graded) larvae, and last in the smallest larvae. With continued development the leg discs of some of the largest and size-graded larvae of the tenth, eleventh and twelfth nomadic days overlap the posterior margin of their thoracic segment and are partially or entirely covered by the surface integument. Consequently, most of the largest larvae of the twelfth nomadic day have no externally visible imaginal leg discs, so that

zero values for leg discs' areas had to be recorded for some of these larvae (table 1).

A graphic representation of the ratios of leg-disc area to body length is given in figure 5 for different times in larval development in the largest, the size-grade (intermediate) and the smallest polymorphic *burchelli* larvae. Leg-disc measurements of larvae of one sample, that of the seventh nomadic day, were excluded from the final analysis of this relation-

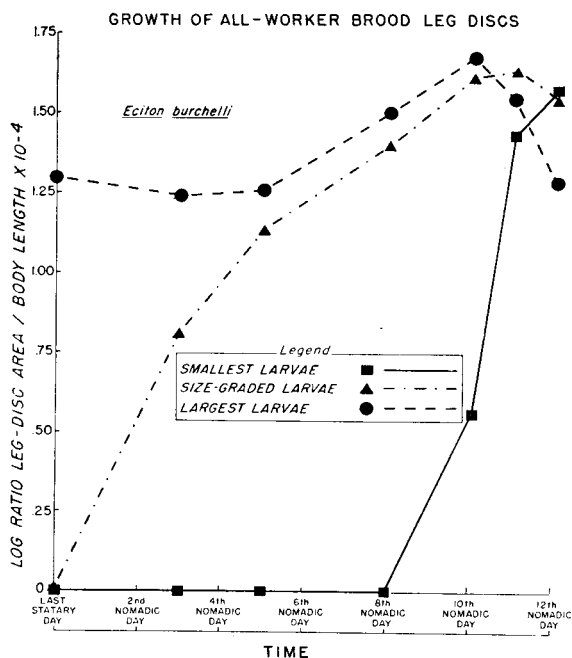


FIG. 5. — Ratio of local and general growth as a function of time throughout larval development in a "synthetic" series representing all-worker broods of *Eciton burchelli*.

last days of the nomadic phase. This last fact is accounted for not only by a proliferation of the leg discs themselves beneath the integument at this stage, but also by a partial overgrowing of the discs by the surface integument.

**F. Other external structures.**—The paired antennal discs are located on the dorso-lateral surface of the head segment (fig. 3). The gonopodal discs, which are paired, and round or oval in shape, are located on the ventral surface of the seventh, eighth and ninth abdominal segments. The discs of the seventh segment are widely spaced on the segment while those on the eighth and ninth segments are situated nearer the midline. Although the antennal and gonopodal discs are relatively small, opaque patches of the hypodermis, in their first appearance and sequence of

ship, since many of these specimens were found noticeably mutilated in the thoracic region. Leg-disc growth rate is indicated by the rate of change in the slope of the line. This graph shows that once leg-disc development is initiated, its growth rate is very different in each of the three groups; it is slowest in the largest larvae, intermediate in the size-graded larvae, and fastest in the smallest larvae. Also shown here is the precocious development of the leg discs in the largest and size-graded larvae during the early and middle days of the nomadic phase, as well as the precocious decrease in leg-disc surface area in these larvae during the

developmental changes throughout larval life, they are closely similar to the imaginal leg discs.

Among other external structures studied in *burchelli* larvae was a holopneustic type of respiratory system which has some of its simple, anastomosing tracheae externally visible through the cuticle. Also in larvae of all sizes, ten pairs of spiracles are present as small, sclerotized, cuticular openings on the dorsolateral surface of the third through twelfth larval segments.

The anal opening is present in all larvae as a transverse slit on the ventral surface of the 14th. segment.

### INTERNAL MORPHOLOGY

General inspection of the polymorphic larval range.—Results from microscopic observations of the internal morphology of larvae through the polymorphic range of any one day's sample do not indicate a linear progression synchronized either in the time of initiation of organ development or in the rate of onset of organ function. With respect to their internal structures, the largest larvae in each day's sample were more advanced in development than were the intermediate (size-graded) or smallest larvae of that sample. In all larvae, the size of the internal organs varies directly with body length, and consequently, a smooth series in the sizes of organs is found between the extremes in body length.

Consideration of all samples throughout development indicates that the onset of activity of the various organs and organ systems is observed first in the largest larvae of each day's sample. However, neither the characteristics of any one internal structure nor of any one tissue could be used to distinguish the various polymorphic forms *per se*.

**A. Alimentary canal.**—The alimentary canal of *burchelli* larvae is essentially a straight tube divided into the foregut, midgut and hindgut (figs. 6, 7, 8, 9, 10, 11 and 12). The foregut extends from its anterior limit at the mouth opening to the region of the metathoracic segment. It proceeds posteriorly as a narrow tube and then reflects upon itself in the prothoracic segment to form the esophageal invagination or cardiac valve. This valve projects into the lumen of the midgut. The foregut is composed of the buccal cavity, the pharynx, the esophagus and the reflected portion of the esophagus, the cardiac valve. The cardiac valve terminates the foregut in the metathoracic segment (fig. 8).

The midgut extends from the mesothoracic segment to the eleventh segment as a large, dilated, blind sac. The midgut is the largest organ of the larva and appears to serve as a mould around which the other abdominal organs are oriented (fig. 6).

The hindgut extends from the blind, posterior limit of the midgut to the ventral surface of the fourteenth segment where it opens to the exterior

at the anal opening. The hindgut is composed of a short, narrow intestine, the expanded rectum and a constricted posterior end, the anus (fig. 9). The four Malpighian tubules are attached to the most anterior portion of the intestine in the region of the twelfth larval segment. The lumina of the mid and hindguts are not continuous until late in the prepupal or early pupal period of metamorphosis.

Once the foregut is established early in larval development, its morphology remains virtually unchanged throughout larval development. In contrast, the midgut appears to be continually changing in its cytological make-up during late embryonic stages, and throughout larval development. The blind, sac-like midgut epithelium is composed of a single layer of extremely large, flat, polygonal-shaped cells (figs. 8 and 11). Early in larval development these cells have distinct round or oval nuclei surrounded by dense, granular cytoplasm. With age, these nuclei become amoeboid in outline and cytoplasmic changes are evident which result in the histolysis of these cells.

In early stages the hindgut is a relatively narrow tube with columnar-shaped epithelial cells, but with further development, the various regions of the hindgut become differentiated (fig. 9). In some of the large larvae of the fifth nomadic day, as well as in the intermediate and smallest larvae of the seventh and all further nomadic days, the hindgut is fully differentiated into intestine, rectum and anal portions. In larvae of all sizes, in the last stages of larval development, the rectum appears to be contracted, and crystalline material, previously observed in the expanded rectal portion of younger larvae, is now evident in the anal portion of the hindgut.

**B. Malpighian tubules.**—In larvae of all sizes, and at all stages of development, the four Malpighian tubules are symmetrically arranged along the dorsolateral and ventrolateral sides of the midgut as two pairs of straight, narrow tubes. These tubes extend anteriorly from their point of attachment on the anterior, dorso-lateral part of the intestine in the twelfth segment, to the region of the fifth or sixth segment and have a rather uniform diameter throughout. The blind, free ends of these tubules are slightly curved, but in the posterior attached region the two ventral tubules are intimately associated with the anteriorly directed branches of the glandular portion of the labial glands.

The Malpighian tubules are composed of a single layer of epithelial cells, roughly cuboidal in shape, which have distinct, ovoid nuclei surrounded by an irregular, fibrillar arrangement of cytoplasm. The inner, free surfaces of these cells are distinctly convex in the largest larvae of the last statary and third nomadic days, as well as in all larvae of further nomadic days (figs. 13, 14 and 15). However, in the smallest and intermediate larvae of the last statary and third nomadic days these cells are more cuboidal in shape.

Throughout larval development the cells of the Malpighian tubules increase in size and show cytoplasmic variations indicative of the functional activity of this organ. With further differentiation, these nuclei

become amoeboid in outline and histolysis of the larval Malpighian tubules is observed only in those larva which have become enclosed in cocoons (i.e. are in the prepupal period of metamorphosis).

In the large larvae of the ninth and tenth nomadic days, the anlagen of the adult Malpighian tubules are arranged in a small cluster around the larval intestine just posterior to the point of attachment of the larval Malpighian tubules (fig. 15).

**C. The nervous system.**—The larval nervous system of *Eciton burchelli* is composed of the central and the stomatogastric nervous systems. The central nervous system consists of the *supra-esophageal ganglion* or *brain*, and a series of twelve, ventrally located, paired *ganglia* of the nerve cord with their respective nerves (figs. 6 and 12). The *stomatogastric nervous system* consists mainly of a median, bean-shaped, frontal ganglion with its anterior bilateral and posterior median nerves (fig. 12).

The *brain*, a pair of large, roughly egg-shaped ganglia, is located in the head segment. These ganglia are almost completely separated medially by a deep, antero-posterior sulcus, across which they are held together by connecting nerve fibre tracts. This *median commissure* is located in the posterior part of the brain just dorsal to the esophagus. At the anterior, ventral region of the brain, three pairs of nerves are evident. The most anterior pair extend to the region of the labium; the middle pair serves as a ventral, interlobular commissure and lies just ventral to the pharynx (fig. 10). The posterior pair extends ventrally and forms the circum-esophageal connectives which join together the supra-esophageal and sub-esophageal ganglia. The ventral interlobular commissure together with the dorsal interlobular commissure form the *circumpharyngeal nerve ring* through which pass the pharynx and esophagus.

The first ganglion of the ventral nerve cord is the *sub-esophageal ganglion*, located ventrally between the head and prothoracic segments (figs. 6, 7, 16 and 17). This ganglion is connected with the second ventral ganglion of the nerve cord, the prothoracic ganglion, by two longitudinal connectives. All successive ventral ganglia are connected similarly, forming a *ventral nerve cord* which has a morphological pattern typical of insect larvae. In the twelfth segment, the last ventral ganglion is relatively large and the nerve tracts within this ganglion unite to form a single, terminal nerve. This nerve projects into the haemocoel of the posterior region of the larvae and branches of it may be clearly seen to reach the rectum and hindgut.

The brain and ventral ganglia are composed of neuroblasts and fibrous tracts. In larvae of early stages, the neuroblasts, which are actively dividing, basophilic-staining cells with dense, ovoid nuclei, are more prevalent than the fibrous tracts (fig. 6). As the larva approach maturity, the abundance of nerve tracts within the nervous system becomes more evident. In the last stages of larval development the brain lobes and ventral nerve cord are highly differentiated into central regions of nerve

tracts and cortical regions of nerve cells (figs. 7 and 10). Throughout development the central nervous system is covered by a nucleated membrane, the neurilemma (figs. 10, 12 and 16).

In all larvae the brain is the most prominent internal organ of the head segment, and its size increases throughout development. In the large larvae of the eighth nomadic day, and in larvae of successive nomadic days, the lobes of the brain extend slightly into the prothoracic segment.

The *frontal ganglion* of the stomatogastric nervous system is located dorsal to the pharynx, just below and in front of the brain lobes. This bean-shaped ganglion has a central core composed of tracts which are surrounded by neuroblasts (fig. 12). Fibers extend bilaterally from the anterior limit of this ganglion, while a single, relatively large, posteriorly directed nerve, the *recurrent nerve*, extends from its posterior limit (fig. 10, 12 and 16). This nerve passes dorsal to the foregut, and many of its branches clearly reach the pharynx, the oesophagus and the oesophageal invagination; *i.e.*, the cardiac valve.

**D. The secretory system.**—1. THE CORPORA ALLATA.—The *corpora allata*, a pair of endocrine glands which from developmental studies of other insects are believed to be associated functionally with the stomatogastric nervous system, are distinctly present in all individuals of the polymorphic series of *burchelli* larvae. In all stages of larval development they are oval, compact lobes of spherical cells, located on either side of the foregut and just posterior to the circumpharyngeal nerve ring (fig. 16). These cells are differentiated into a central core of densely basophilic-staining cells surrounded by a slightly less dense, basophilic-staining peripheral region. The cells of both regions have distinct ovoid nuclei surrounded by granular cytoplasm.

The corpora allata are surrounded by a network of tracheoles and are suspended in the blood sinuses by these tracheoles and nerves of the central and stomatogastric nervous systems. In the materials studied, in larvae of the different polymorphic size groups, the corpora allata were distinguishable only in size, which in all cases seems to be directly proportional to the overall size of the individual larva.

2) THE LABIAL GLANDS.—Throughout the course of larval development in the worker broods of *Eciton burchelli*, a series of significant morphological and histological changes of the labial glands is apparent. These changes evidently result in the two-fold functional activity of this gland; first, as the site of production of the labial secretion, and second, as the site of production and accumulation of the precursor of the spinning silk. Histological signs of the onset of activity of the labial glands, and of their subsequent change in function, are always observed first in the largest polymorphic size larvae, second in the intermediate larvae, and last in the smallest larvae. The 'phase-day' age at which the functional activity of these glands begins evidently is one of the factors underlying differential

growth and development among larvae of the different polymorphic groups and is believed by SCHNEIRLA to be related to the amount of stimulative and trophic exchange between adults and brood resulting in varied levels of colony excitation.

The labial glands of mature *burchelli* larvae are bilaterally arranged, branched, tubular structures which lie ventral and lateral to the alimentary canal, and open on the labium. They are divided into the duct portion, the saccus portion, and the glandular portion, and extend from the labium to the eleventh or twelfth larval segment. These glands are the sericteries or spinning glands of the larva, and the terminology adopted here for their various portions is in agreement with that previously used for *Myrmica schencki* by STÄRKE (1948) and for *Eciton hamatum* by TAFURI (1951).

The duct portion of this gland is divided into the common duct of the labial gland and the paired branches of this duct, the ducts of the labial gland. The common duct extends from the opening on the labium to the prothoracic segment, where the ducts of the labial gland are also located. Each saccus portion extends from the posterior region of the prothoracic segment to the fifth or sixth segment; each glandular portion extends from this region to the tenth or eleventh segment where it branches dichotomously. One branch extends posteriorly to the twelfth segment where it terminates as a blind tube; the other turns dorsally and proceeds anteriorly to the region of the seventh or eighth segment, where it too terminates blindly.

In mature larvae of all the polymorphic size groups the three portions of the labial glands differ histologically although the entire gland is composed of simple epithelium arranged on a distinct basement membrane. During early larval development, however, the saccus and glandular portions are nearly identical and are composed of simple, cuboidal shaped cells. The lumina of the saccus and glandular portions at this time are extremely narrow and of uniform diameter (figs. 13 and 18). The duct portion is composed of high cuboidal-shaped cells which surround a distinct lumen (fig. 18). This early stage of labial gland development is found in all the smallest and in some of the intermediate larvae of the last statary day, and in some of the smallest larvae of the third and fifth nomadic day's samples.

In the largest and some of the intermediate size larvae of the last statary day, and in some of the larger of the intermediate and smallest larvae of the third and fifth nomadic days, the lumen widens at the posterior end of the glandular portion of the labial gland and the cells surrounding it appear larger than in larvae of the respective types at earlier stages. These cells are rather vacuolate at their outer, attached border, and the lumen they surround contains small amounts of a fine, basophilic-staining, granular secretion (fig. 19). The cells of the saccus portion at this time are gradually becoming flatter to assume a low, polygonal shape (fig. 17). Small amounts of the secretory material are

observed in the lumina of the saccus and ducts of the gland at this time, indicating the onset of secretory activity of these labial glands.

An increased secretory activity of the cells of the glandular portion occurs with development. The cells appear more vacuolate at their outer, attached borders while at their inner, free borders the presence of secretory material is evident (fig. 20). The cells of the saccus portion, now squamous in shape, have a uniformly granular cytoplasm. This condition is observed first in the labial glands of some of the largest larvae of the third nomadic day, in the intermediate and smallest larvae of the fifth nomadic day, and occasionally as late as in the smallest larva of the tenth nomadic day.

The height of secretory activity of the labial gland is marked by an increase in the amount of fine, basophilic-staining, secretory material in the lumina of the glandular, saccus and duct portions (figs. 7 and 21). This condition, observed first in some of the largest larvae of the fifth nomadic day, next in the size-graded larvae of the seventh nomadic day and last in some of the smallest larvae of the eighth and tenth nomadic days, is found in all older and more advanced individuals of the respective groups. It persists until the function of this gland changes from the production of the labial secretion to the production of the precursor of the spinning material. This change in function of the labial gland from its primary to its secondary role is noted first in some of the largest larvae of the eighth nomadic day, and next in the largest, the intermediate and some of the smallest larvae of the tenth and eleventh nomadic days. At this time the cells of the glandular portion become enlarged, irregular in shape and stain intensely basophilic (fig. 14). At the correspondingly different times noted above, the lumen of this region becomes almost completely obliterated.

Somewhat later than the last noted time, a fibrous-appearing acidophilic substance begins to accumulate in the lumen of the glandular portion. This is observed in some of the largest larvae of the tenth nomadic day, and in the intermediate and smallest larvae of the eleventh and last nomadic days. This substance, believed to be the precursor of the spinning silk, accumulates first at the terminal ends of the glandular portion and then more anteriorly. The cells surrounding this fibrous material are now low, cuboidal-shaped, deeply staining basophilic cells which have a dense granular cytoplasm (fig. 15). At this stage of labial gland development, the cells of the saccus portion show signs of a cellular breakdown and irregular, coarse, basophilic-staining masses become evident in the lumina of the saccus and ducts (fig. 22 and 23).

To summarize the developmental history and functional activity of the labial glands, corresponding changes in the formation of products of the labial gland occurs in the three arbitrary polymorphic groups at respectively different times in the nomadic phase. At the last statary and early nomadic days only the largest larvae have glands producing salivary secretion. As the nomadic phase proceeds, the size-graded and the smallest larvae acquire functional glands, until at the seventh or eighth nomadic day almost all individuals of the three arbitrary size groups have functional



labial glands capable of a maximal secretory activity. This secretory condition persists until the time when acidophilic spinning material begins to form in the glandular portion simultaneously with the disintegration of the saccus portion of the labial gland. This is evident in the largest larvae of the tenth and eleventh nomadic days and in the smallest larvae on the twelfth nomadic day. The passage of the spinning material to the ducts of the gland occurs in the very last stages of larval development just prior to cocoon spinning and is evident in some of the largest larvae of the twelfth nomadic day. Some of these largest larvae are then already enclosed in cocoons, thus indicating their precocity in this and related aspects of development.

**E. Imaginal leg discs.**—Histological study of sectioned materials supports the conclusions from microscopic examinations and measurements of the external morphology of *burchelli* larvae as to the imaginal leg discs, concerning the time of their first appearance, relative size at different stages, pattern of development, and rate of growth. Judgments regarding development of the leg discs of the more mature larvae of the tenth, eleventh and last nomadic days were also verified by study of the internal morphology of these structures.

The leg discs first appear as paired thickenings of the hypodermis on the ventral surface of the thoracic segments (fig. 18). These structures are composed of several layers of actively dividing, basophilic-staining cells. In the course of development these discs become set off from the surrounding hypodermis by a peripodal cavity (fig. 7). As they grow, the leg discs undergo an antero-posterior extension as well as a transverse segmentation, with a corresponding enlargement of the peripodal cavity (figs. 22 and 24). The leg discs are in their most advanced state of development in the potential major worker larvae at the tenth nomadic day, in the intermediate larvae at the eleventh nomadic day, and in the smallest larvae at the last nomadic day. In this condition they are large, elongated, transversely segmented structures, generally submerged beneath the surface of the integument. Each of the three pairs of leg discs lies for the most part within one thoracic segment, but at maturity the posteriorly directed free ends of all the pairs usually extend into the next segment (fig. 24).

As the leg discs grow and become more posteriorly directed, there is a decrease in their visible surface area for they grow beneath the integument and the surface integument grows over the discs so that only a small portion of each leg disc projects above the integument. These projecting structures have been studied in detail by G. C. WHEELER (1938) who termed them 'leg vestiges'. These occurrences in leg disc development account for the fact that first in the largest and then in the upper intermediate size groups after the tenth nomadic day, no values for external leg disc areas can be recorded (table I). From this we should also expect a resulting drop in the curve representing *burchelli* leg-disc growth in terms of external measurements in the last stages of larval development (fig. 5).

**F. Dorsal vessel.**—The dorsal vessel or heart of *burchelli* larvae is a single median tube which lies just under the dorsal integument and is

surrounded by many pericardial cells, fat tissue cells and muscles. In its forward extension from its open posterior end, it first lies above the rectum in the region of the twelfth or thirteenth segment, extending to its anterior aortic region in the prothoracic segment. Here the heart bifurcates to form two anteriorly directed branches which extend ventrally into the head segment, where, after flanking the walls of the esophagus, each terminates on the side of the esophagus just dorsad to the corpora allata. These branches of the heart seem to terminate in a sinus, the fluid contents of which presumably bathe the corpora allata, the brain and other head structures.

In this species, the ostia of the dorsal vessel are found in each segment, dorsolaterally arranged, and appear to form valve-like septa. As each intersegmental region of the heart apparently is enlarged in its diameter, the heart takes on a chambered appearance.

Histologically, the heart is composed of a single layer of extremely flattened, endothelial-like cells, and its walls are surrounded by numerous minute muscles and nerves. This organ is much the same in all stages of larval development and in larvae of all the different polymorphic size groups. However, in the larvae studied, different states of contraction of the heart are evident which may be assumed to reflect its physiological condition at the time of fixation.

**G. Ovaries.**—The undeveloped ovaries of *burchelli* larvae are discernible as paired, elongated, strap-like bodies located in the middorsal region of the ninth or tenth larval segment lying between the heart and midgut. These primordia of the evidently non-functional reproductive system of the adult worker are present in larvae of all polymorphic size groups throughout development. They are extremely minute in larvae of the early developmental stages, but as development continues, mitotic divisions are evident in the ovaries and they enlarge. Two distinct regions become discernible; a central core of basophilic-staining cells, and a periphery of acidophilic-staining cells (fig. 25). The cells of both regions have distinct ovoid-shaped nuclei. The ovaries are surrounded by a fibrous network, but no oviducts or genital openings were apparent in any of the material studied.

**H. Fat tissue.**—Numerous fat cells are present in *burchelli* larvae throughout development, and a general judgment was made of the relative amount of fat present within larvae of the different polymorphic forms at different stages of development. The results of these observations indicate that the largest larvae at each successive developmental stage have relatively greater amounts of fat tissue than do either the intermediate or the smallest larvae of that same developmental stage, or the intermediate or smallest larvae of comparable body length at other developmental stages.

Apart from differences in the relative amounts of fat tissue in larvae of the different polymorphic size groups, changes were noted in the

cytology of the fat cells in larvae of all sizes throughout development. These changes include the presence, in varying amounts, of vacuoles, acidophilic-staining globules, and crystalline inclusions in the fat cells (fig. 7, 13, 15, 18, 20 and 23). These changes are believed indicative of, and related to, metabolic changes during metamorphosis of this species, but not to polymorphic differences.

## DISCUSSION

The description of the external morphology of *Eciton burchelli* herein presented conforms to and extends the general descriptions given for larvae of this species by EMERY (1899 and 1901) and G. C. WHEELER (1943). Study of the internal anatomy of the larva of this species reveals a close similarity to that of *Eciton hamatum* (TAFURI, 1951) and a general similarity to the anatomy of other ant larvae which have been described from histological studies (PÉREZ, 1902; STÆRKE, 1948; ATHIAS-HENROIT, 1947; MARCUS, 1951, and VALENTINI, 1951). The present account also confirms the brief description of the digestive tract of *Eciton burchelli* made by WHEELER and BAILEY (1925).

Adult worker populations of *Eciton burchelli* are polymorphic (W. M. WHEELER, 1910 and 1921, and EMERY, 1899). That is, all the adult individuals of a single *Eciton* colony are sterile females which between the extremes exhibit graduated differences in body size and in structural details. The adult extremes range from the largest workers, the workers major, which have huge hooked mandibles and a heavy exoskeleton, to the smallest workers, the minima, which have relatively small, feebly developed mandibles and a less heavily armored exoskeleton.

It is highly probable that the largest larvae of any stage have developed from the eggs first to be laid and first to hatch and represent the potential major workers of the mature brood. Similarly, the smallest larva presumably develop from the eggs last to be laid and last to hatch and represent the potential workers minima of the mature brood.

Study of the development of a single *hamatum* brood series (TAFURI, 1951 and 1955) revealed a distinct foreshadowing of adult polymorphism in the larval form. For example, evidence was found that during larval development the growth of the imaginal leg discs proceeds at a different rate in each of the three polymorphic size groups studied. TAFURI's results show that the growth rate of specific larval structures is describable as an allometric and not as a direct function of the overall body growth. His results showed that in *hamatum* larvae the growth rate of the leg discs was slowest in the largest larvae, intermediate in the intermediate size larvae, and fastest in the smallest larvae of the developing brood. In all three of these polymorphic types, the leg discs being the local structures best studied in this connection, the limb buds advance in a geometric

and not in a direct relationship to body length when body length is taken as the indication of overall body growth.

The evidence presented in this investigation regarding larval development of a synthetic series of all-worker brood of *Eciton burchelli* indicate that differences exist in hatching time within the distinctive brood, as well as growth differences in size and in the time at which individuals throughout the size range attain specific structural advances. From these results it is apparent that from the earliest stages of development the basis of adult polymorphic differences is established in the brood of this species.

It is significant that differences in the growth pattern of the leg discs occur in *burchelli* much as TAFURI found them to occur in *hamatum*. Also, for *E. burchelli* the ratio of quantitative changes in leg discs to body length was obtained for each of the three larval groups through the

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Fig. 1-7. — (1) Fig. 1. Representative specimens of the smallest (A), the size-graded (B), and the largest (C) polymorphic size-groups of *Eciton burchelli* larvae. 11th N. D.\* Lynch's borax-carmines whole mount. X 1.75. Fig. 2. Dorsal view of head segment showing mouth parts. L-larva\*\*, 7th N. D. Lynch's borax-carmines whole mount. X 55. Fig. 3. Side view of head and prothorax showing mouth parts and some internal structures. I-larva\*\*\*, last N. D. Lynch's borax-carmines whole mount. X 80. Fig. 4. Ventral surface of larva showing imaginal leg discs (two pairs, meso and metathoracic, in focus) and one leg vestige (mesothoracic). L-larva, 8th N. D. Bouin's preserved specimen. X 4.75. Fig. 6. Longitudinal section. S-larva\*\*\*\*, 3rd N. D. Harris' haematoxylin, eosin. X 80. Fig. 7. Longitudinal section of head and thorax. I-larva, 8th N. D. Harris' haematoxylin, eosin. X 55.

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#### LEGEND TO FIGURES

A : Anus. — AD : Antennal Disc. — B : Brain (Supraesophageal ganglion). — BC : Buccal Cavity. — Bl : Blood. — Bl' : Blood (Very granular). — CA : Corpora Allata. — CB : Cellular Breakdown products. — CD : Common Duct (Labial Gland). — Ch : Chorion. — Cu : Cuticle. — Cu' : Cuticle (Double). — DL or LD : Duct Labial Gland. — DV : Dorsal Vessel (Heart). — E : Esophagus. — EI : Esophageal Invagination (Cardiac Valve). — F : Fat. — FM : Fibrous Acidophilic Material. — FG : Frontal Ganglion. — G : Galea. — GD : Gonopodal Disc. — GL or LG : Labial Gland (Glandular Portion). — Gr : Granular Secretion (Labial). — H : Hypodermis. — Hg : Hindgut. — I : Intima. — L : Lumen filled with fine granules. — Lb : Labium. — LD : Leg Disc. — LP : Labial Palp. — Lr : Labrum. — LV : Leg Vestige (Sectional view). — LV' : Leg Vestige (Small circular structure). — M : Midgut. — M' : Midgut (Histolysis). — Md : Mandible. — MT : Malpighian Tubules. — MT' : Anlagen of Adult Malpighian Tubules. — Mu : Muscles (Surrounding Midgut). — Mu' : Muscles (Surrounding Esophageal Invagination). — Mx : Maxilla. — MxP : Maxillary Palp. — NC : Ventral Nerve Connectives. — Nu : Neurilemma. — O : Ovary. — OS : Opening of Sericteries (Labial Glands). — P : Pharynx. — PG : Peripodal Cavity. — PG : Prothoracic Ganglion. — PM : Peritrophic Membrane. — PS : Prothoracic Segment. — R : Rectum. — RN : Recurrent Nerve. — S : Saccus (Labial Gland; Sectional view of cells). — S' : Saccus (Labial Gland; Surface view of cells). — SG : Subesophageal Ganglion. — Su : Submerged Portion of Leg Disc. — VG : Ventral Ganglion. — VG' : Ventral Ganglion (Last).

\* N. D. -- "Nomadic Day".

\*\* L-larva of the largest polymorphic size group.

\*\*\* I-larva of the size-graded (Intermediate-size) polymorphic size group.

\*\*\*\* S-larva of the smallest polymorphic size group.

(1) All illustrations are photomicrographs of *E. burchelli* larvae.

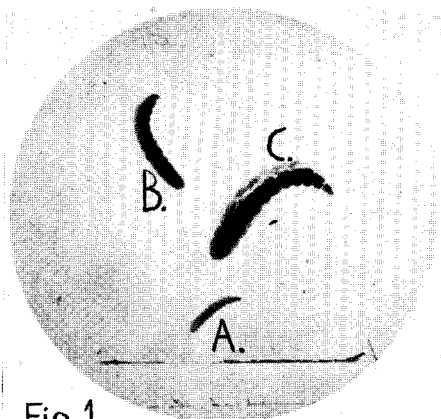


Fig. 1

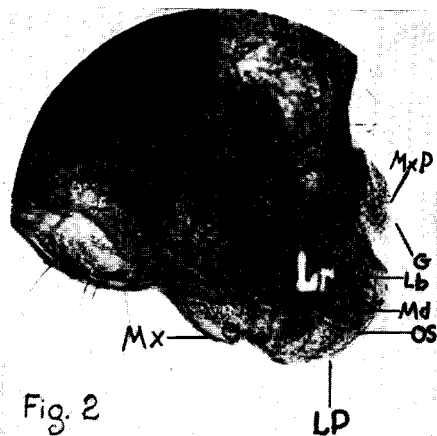


Fig. 2

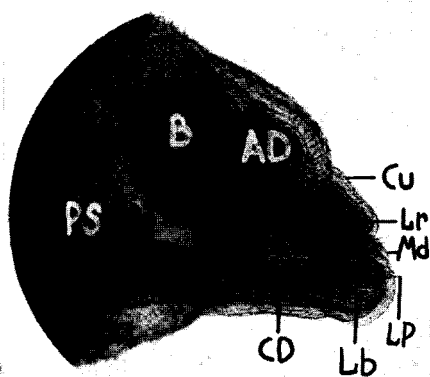


Fig. 3

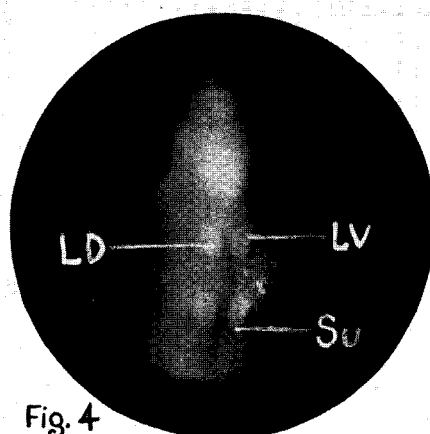


Fig. 4

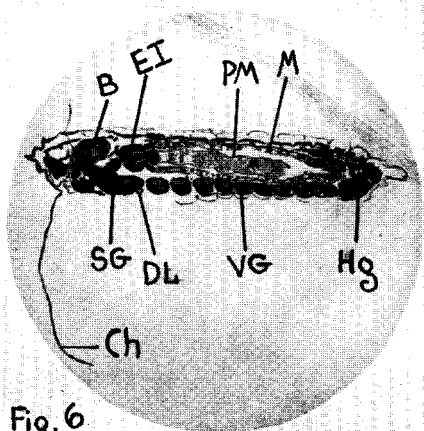


Fig. 6

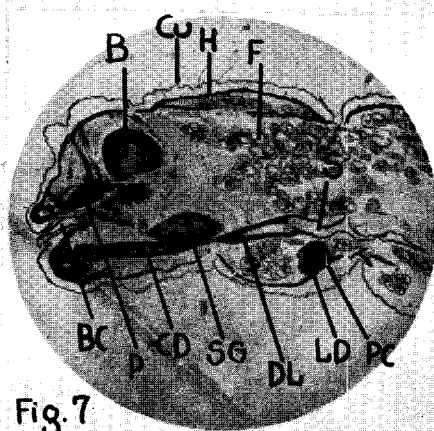


Fig. 7

polymorphic range. A graphic expression of the results indicates that the allometrically expressed growth rate is characteristically different for individuals through the polymorphic series, being slowest in the largest, somewhat greater in the intermediate and most rapid in the smallest larvae. These results might have been expected from SCHNEIRLA's (1933) confirmation and extension of MÜLLER's (1886) single observation that in *E. burchelli* the worker majors are the first individuals in each brood to eclose, the workers minima last. SCHNEIRLA (1949) has also reported that in *E. burchelli* and *E. hamatum* similar conditions prevail as to the attainment of larval maturity and enclosure in the respective polymorphic types.

The type of continuous, evenly graduated polymorphism found in the all-worker broods of these Ecitons may be understood in the light of previous studies of polymorphism of the intra- or inter-caste type which it resembles. The characteristic unique to the Ecitons, as SCHNEIRLA (1938 and 1949) has emphasized, is the occurrence of such polymorphism through very large, distinctive brood populations produced at regular and well-marked intervals throughout the year.

Differing theories have been proposed regarding the cause and time at which caste determination occurs during development of the social insects and reviews of the literature on this topic (LIGHT, 1942 *a*, 1942 *b*; W. M. WHEELER, 1908, 1910, 1933; and WILSON, 1953 *a*, 1953 *b*) draw attention to two main approaches to the solution of this problem. Caste determination may be considered to be mainly or entirely blastogenic, being established by genic factors and by the amount and quality of nutritive material in the egg and embryo (W. M. WHEELER, 1933; FLANDERS, 1946 and 1952), or it may be considered to be trophogenic and due to the quality or quantity of the diet during larval development, trophic exchanges between the adults and the developing broods being the determining factors (W. M. WHEELER, 1910 and 1933, and WILSON, 1953 *a*). A blastogenic determination, on the other hand, might be regarded as restricted to genic factors alone. More recently there has been a tendency to consider both the trophogenic and blastogenic factors as contributors to the caste determination of ants (FLANDERS, 1945). In any event, it is generally accepted that caste determination begins to be established prior to the histolytic and histogenetic processes of the pupal period of metamorphosis.

Recent experimental advances bearing upon caste determination and

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FIG. 8-13. — *Fig. 8.* Longitudinal section through head and thorax of brood specimen. L-larva, 8th N. D. Harris' haemotoxylin, eosin. X 55. *Fig. 9.* Longitudinal section through posterior abdomen. I-larva, 5th N. D. Harris' haemotoxylin, eosin. X 55. *Fig. 10.* Transverse section through head. S. larva, 7th N. D. Harris' haemotoxylin, eosin. X 265. *Fig. 11.* Transverse section through abdomen. I-larva, 8th N. D. Iron alum haemotoxylin. X 55. *Fig. 12.* Longitudinal section through head. L-larva, 8th N. D. Harris' haemotoxylin, eosin. X 265. *Fig. 13.* Longitudinal section through abdomen. I-larva (Near small), 5th N. D. Harris' haemotoxylin, eosin. X 265.

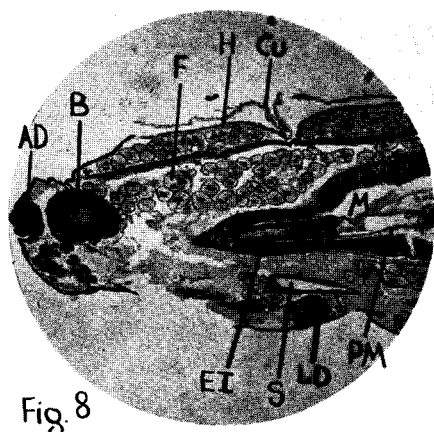


Fig. 8

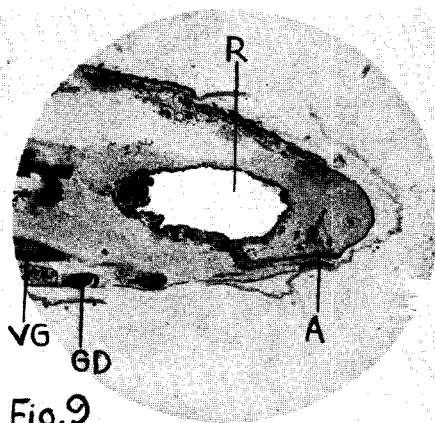


Fig. 9

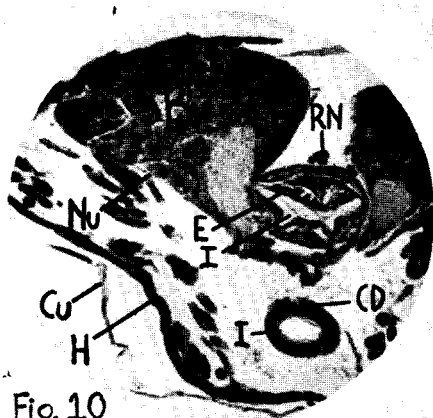


Fig. 10

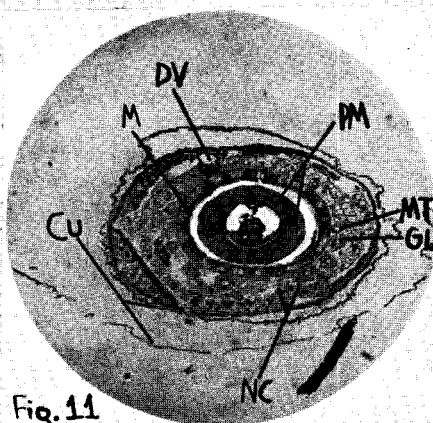


Fig. 11

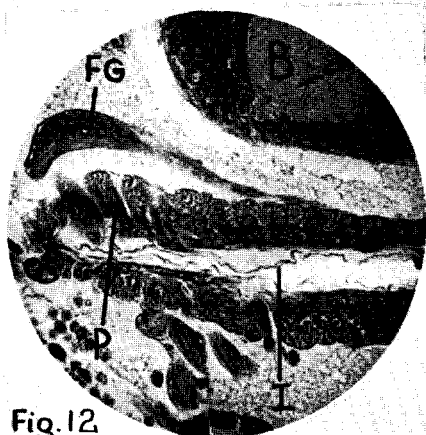


Fig. 12



Fig. 13

polymorphism of the intercaste type in the social insects suggest that the caste of any individual is set during larval development and that nutrition and the attained size of the larvae at the time of pupation are its major determinants (WILSON, 1953 *a*, 1953 *b*). BRIAN (1951, 1952) from studies of caste determination in *Myrmica rubra*, finds results indicating that larval size at pupation, along with the size and state of development of the imaginal rudiments, particularly the leg discs, are critical to determination of queen or of worker castes.

In *E. burchelli* and *E. hamatum*, queens and workers occur in distinctively different broods as SCHNEIRLA and BROWN (1952) have reported. These investigators find indications of a differentiation established very early in development, apparently on a trophic basis. SCHNEIRLA considers it very probable that polymorphic differences in the all-worker broods may depend mainly, if not altogether, on graduated differences in trophic conditions affecting different parts of the brood series. These differences in trophic conditions could possibly depend upon differences in the order of the oöcyte maturation process, egg-laying and hatching of the eggs, and upon the time at which larval feeding begins. From field observations, he estimates that a queen of *Eciton burchelli* requires a period of about ten to twelve days to lay the more than 120,000 eggs of the distinctive all-worker broods of this species, with an intermediate peak of 3 to 4 days.

In the present studies of the larval stages of development in these all-worker broods, beyond relative differences in the overall size, size of the corresponding structures and relative differences in the time of appearance of these structures in the various members of the brood series, no evidence was found of qualitative differences in external or internal structures through the polymorphic range. However, throughout the larval series at any one time, the differences in size and volume of the larvae are consistent with what would be expected from the study of brood samples from the same brood at any earlier time. That is, in all cases, the largest larvae, presumably developed from eggs first laid and first hatched in the series, are the first to develop local structures such as the leg discs and functional organs such as the labial glands, and are the first to exhibit the respective changes of further growth in these structures. From these differences it may be concluded that the largest larvae reach each further growth stage upward to and including larval maturation, as well as

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FIG. 14-19. — *Fig. 14.* Longitudinal section through abdomen showing intensely basophilic-staining cells of the granular portion of the labial gland. L-larva, 10th N. D. Harris' haemotoxylin, eosin. X 265. *Fig. 15.* Longitudinal section through abdomen of L-larva, 10th N. D. Harris' haemotoxylin, eosin. X 55. *Fig. 16.* Transverse section through posterior region of head. I-larva, 3rd N. D. Iron alum haemotoxylin. X 265. *Fig. 17.* Longitudinal section through thorax. I-larva (near large), last Statory day. Harris' haemotoxylin, eosin. X 265. *Fig. 18.* Longitudinal section through prothorax. I-larva (near small), 5th N. D. Harris' haemotoxylin, eosin. X 265. *Fig. 19.* Longitudinal section through abdomen. I-larva (near large), last statory day. Harris' haemotoxylin, eosin. X 265.



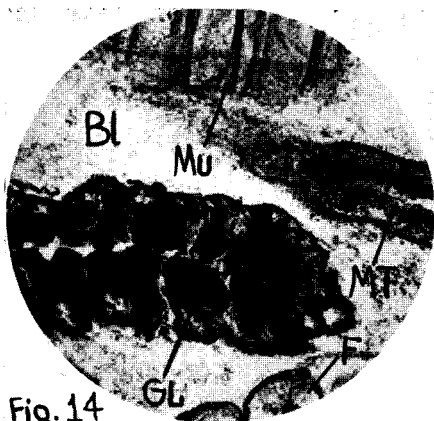


Fig. 14

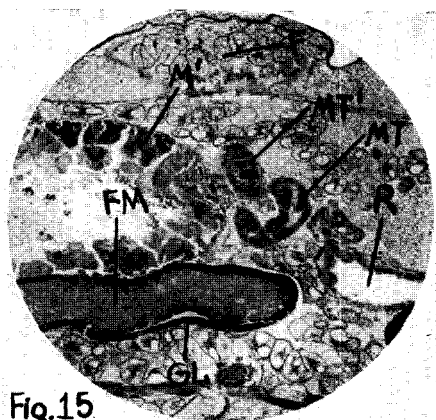


Fig. 15

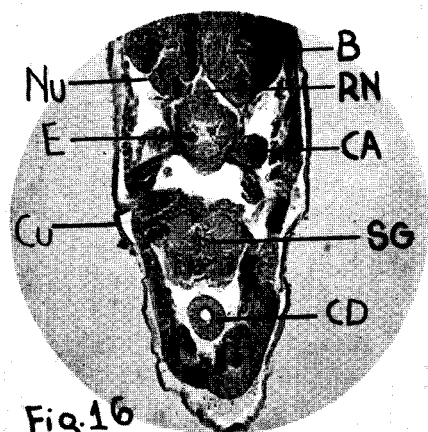


Fig. 16

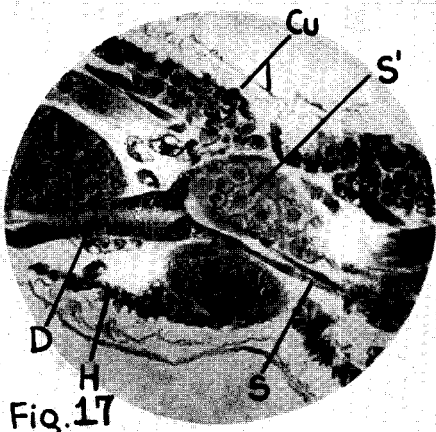


Fig. 17

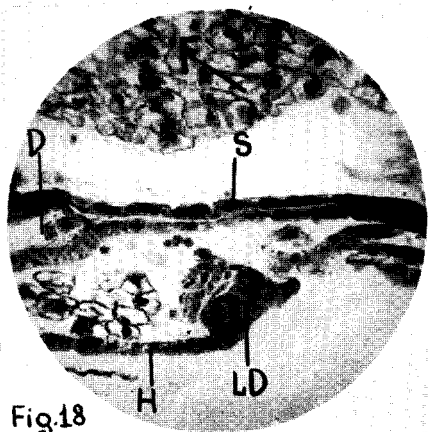


Fig. 18

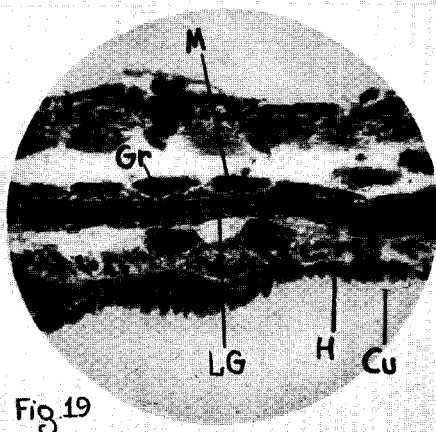


Fig. 19

spinning, in advance of the rest of the brood series. Conversely, the smallest larvae reach their fully mature state last. This statement is confirmed in some detail by evidence from the present study.

In *burchelli* the leg discs appear first in the largest larvae (last statary day), next in the intermediate larvae with roughly corresponding body size (third and seventh nomadic days), and lastly in the smallest members of the polymorphic series (eighth or tenth nomadic days). An inclusive period of about ten days is thus required for the onset of this growth change to occur in all larvae of the series. The further pattern of growth and development of *burchelli* leg discs, marked by changes such as the formation of a peripodal cavity and transverse segmentation, is similar to that previously described for other hymenoptera (PACKARD, 1897, and PRATT, 1897). Due to the fact that these structures become located beneath the surface of the integument as larval maturation approaches in *burchelli* broods, the externally visible and measurable areas of these structures then steadily diminish to a minimum.

Comparisons of larval development of *Eciton burchelli* here studied with that of *Eciton hamatum* (TAFURI, 1955) disclose only minor differences in the growth pattern of homologous structures such as the leg discs. The discs grow similarly in both species as to the increase in size, appearance of segmentation and overlapping of the posterior margins. However, one consistent difference is that in the larvae of *hamatum*, the leg discs do not grow beneath or submerge beneath the surface of the integument to any appreciable extent prior to larval maturation as they do in *burchelli*. In *hamatum* larvae increases in the size of these structures are thus externally perceptible up to the time of enclosure. The described species difference in the pattern of leg-disc growth may be related to still other differences which exist between the two species, such as variations in developmental stage among the larvae of any one cross-sectional sample. A comparative study of *E. burchelli* and *E. hamatum* in the growth rate and pattern of development of leg-disc structures will be presented in a further publication.

In the larvae of *Eciton burchelli*, the rate of growth of the leg discs is different from the overall growth rate, and is specific to this local structure. Growth of this type has been described as disharmonic or allometric growth (WIGGLESWORTH, 1950).

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FIG. 20-25. — Fig. 20. Longitudinal section through abdomen. S-larva, 10th N. D. Iron alum haemotoxylin. X 265. Fig. 21. Longitudinal section through glandular portion of labial gland in abdomen. L-larva, 8th N. D. Harris' haemotoxylin, eosin. X 265. Fig. 22. Longitudinal section through thorax showing part of submerged leg disc and disintegrating saccus portion of the labial gland. S-larva, 11th N. D. Harris' haemotoxylin, eosin. X 265. Fig. 23. Longitudinal section through thorax larval specimen showing cellular breakdown of saccus. Largest larva, 10th N. D. Harris' haemotoxylin, eosin. X 265. Fig. 24. Longitudinal section through thorax showing intact imaginal leg disc amid histolyzing tissues. L-larva, 12th N. D. Harris' haemotoxylin, eosin. X 55. Fig. 25. Longitudinal section through ovary of mature worker larva. L-larva, 10th N. D. Harris' haemotoxylin, eosin. X. 265

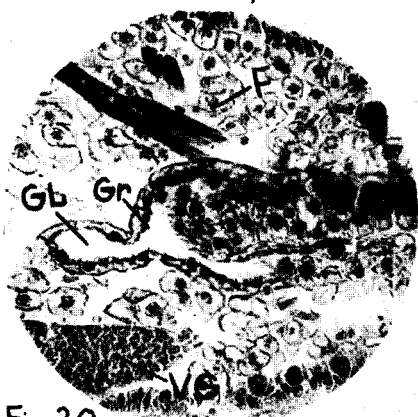


Fig. 20

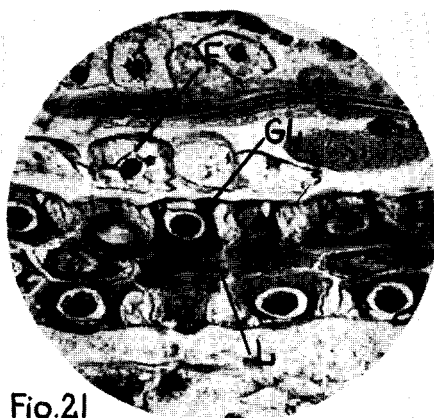


Fig. 21

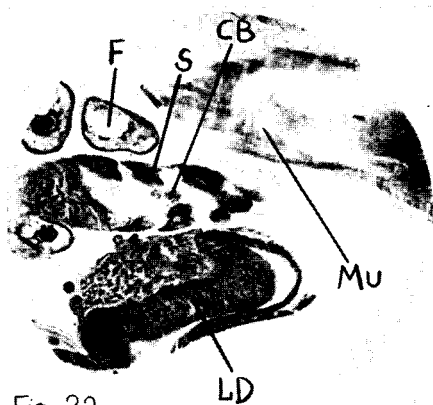


Fig. 22

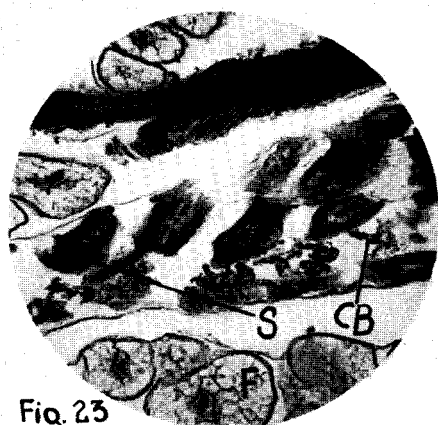


Fig. 23

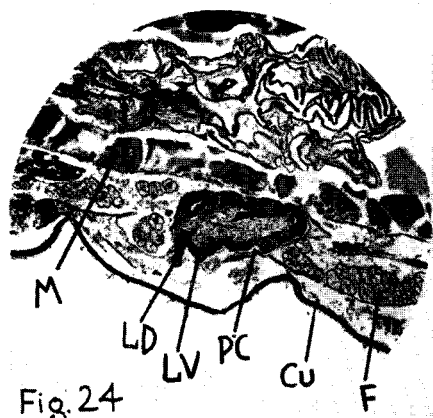


Fig. 24

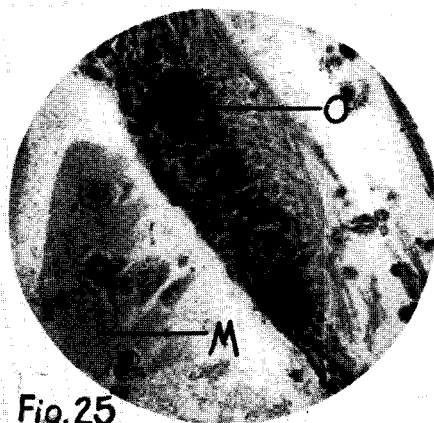


Fig. 25

Analysis of measurements of the different parts of organisms, particularly of arthropods, comparing the relative growth of these parts to the whole, have been carried out by many investigators. In 1932, HUXLEY demonstrated that a mathematical relationship exists between the growth of a part of an organism and the growth of the whole organism. He expressed this relationship in the heterogony formula,  $y = bx^k$ . Later this formula was termed the allometry formula and was revised to  $y = bx^a$  (HUXLEY, 1936) in which  $y$  equals the dimension of the part,  $x$  the dimension of the whole, and  $b$  and  $a$  are growth constants. HUXLEY showed that numerous measurements of the growth of crustacean parts, when compared to the whole, verified an allometric growth in these organisms represented by this formula. He was also able to establish the fact that polymorphism in the neuter individuals of social insects is comparable to the allometric growth of other arthropods and that his formula may be applied to both neuter social insects and arthropods in general. HUXLEY further postulated that apparent differences in structure, such as the size of the head and mandibles, among the various polymorphic forms of the social insects was a product of differential growth rate of the corresponding larval parts.

Because the present investigation utilized a synthetic population series from all-worker broods of *Eciton burchelli* in the larval period of development, the reliability of these results must be evaluated in terms of possible inter-colony differences. Possible differences effecting the growth situation, sampling techniques and relative food supplies are considered to be of major concern.

Obtaining reliable brood samples from *Eciton* colonies is difficult under the best conditions in the natural situation, in which numerous complex factors such as a gradient-wise brood distribution in the bivouac (SCHNEIRLA, BROWN and BROWN, 1954) are inevitably involved. From a general comparison of the species it seems probable that such factors impede sample reliability somewhat more extensively in the case of *E. burchelli* than in *E. hamatum*. It is therefore important to this discussion to emphasize TAFURI's (1951) findings, confirmed in this study, from studies confined to samples from a single brood series of *hamatum* which show that the relationship of overall growth to that of the local structure is expressible for that species in terms of the HUXLEY allometry formula.

By analogy, the same conditions may hold in general for *burchelli*, although with secondary differences to be expected in view of species differences such as colony and brood size, the detailed pattern of the brood microclimate in the bivouac and the like. Our present application of the allometry formula to *burchelli* may be considered too severe a test, particularly in view of the fact that the necessary use of a 'synthetic brood series', assembled from different colonies, must have magnified greatly the normal intercolony differences affecting the reliability of brood samples. For this reason it is probable that the quantitative results concerning the relationship between body length and leg-disc size were somewhat too

widely spread for a convenient statistical treatment. When an analysis of a single brood series can be made for *burchelli*, it is to be expected that much the same condition will be found for that species as for *hamatum*.

The developmental changes in the labial glands of *Eciton burchelli* larvae herein described are not unique to this species and closely parallel those described by VALENTINI (1951) for *Componotus silvaticus*, also a cocoon-spinning form. VALENTINI investigated the morphological variations of different species of ant larvae in collection with species adaptations to arid, normal or humid environments. According to him, the various morphological modifications and functional properties of the labial glands during larval development are related to the type of life situation characteristic of the species, whether the pupa is open or closed, or more specifically, whether the species is a cocoon-spinning form or not. VALENTINI concluded that apparent changes in activity of the labial glands were not directly related to the environmental conditions, but rather to the phylogenetic position of the particular species being studied. However, these may not prove to be real alternatives.

The importance of the labial glands in the social insects has long been recognized. To then W. M. WHEELER (1910) and others have attributed an important role in the trophic processes of the social insects. The times at which these glands first become functional in *burchelli* larvae, and their two-fold production of first a fine, basophilic-staining secretion and secondly, the precursor of the spinning material, suggest that the function of these glands is involved to an important extent in the brood-stimulative effects found by SCHNEIRLA (1938, 1952) to be critical for major changes in the colony behavior cycle.

Behavioral studies of *Eciton hamatum* and *Eciton burchelli* by SCHNEIRLA (1938, 1957) revealed that a distinctly increased level of colony excitation, manifested by the onset of adult predatory raids and greatly augmented 'trophallactic' relations between brood and adults, begins at the end of the statary phase, continues into the nomadic phase, and reaches its peak at larval maturity, a day or so before cocoon spinning occurs. The stimulative effect of the brood on the colony then drops away very sharply, and after the first few days of the next statary phase reaches a minimum with a limited rise near the end of the statary phase (SCHNEIRLA, 1952). At the end of this phase, emergence of the callows occurs, and once again a sharp increase in colony stimulation occurs, with colony nomadism as its main effect.

The nomadic phase in *E. hamatum* has a mode of 16 days while that of *E. burchelli* is three to four days shorter and more variable. It has also been established that the peak of raiding activity resulting in an over-abundant food supply begins at an earlier 'phase-day' age in *burchelli* colonies, that is, at approximately the eighth or ninth nomadic day. In *hamatum* this peak in raiding activity begins at approximately the twelfth or thirteenth nomadic day.

In *E. burchelli* the labial glands first become functional in the largest

larvae of the last statary and early nomadic days. Soon afterward, the intermediate and smallest larvae of successive nomadic days have functional labial glands, and by the seventh or eighth nomadic day all larvae of the different polymorphic size groups have functioning labial glands producing salivary secretion. Although the significance of this labial (or salivary) secretion for trophic and stimulative relations between brood and colony remains to be worked out, it is of interest to note that the time at which labial gland function rises to a high level coincides with the beginning of a peak of raiding activity indicated for this species at the eighth or ninth nomadic day. Furthermore, it is significant that the change in function of this gland from its primary secretory function to the production and accumulation of the precursor of the spinning material begins in the largest larvae on the tenth nomadic day, and in the intermediate and smallest larvae on subsequent nomadic days. This coincides with the time at which these respective polymorphic forms are observed to drop off in their feeding activities, although the stimulative effect of the larval brood on the adult population remains at a high point until the major part of the brood is enclosed. These results regarding larval feeding activities were obtained from field observations and laboratory studies of *E. burchelli* by SCHNEIRLA (1949).

The significance of these developmental changes in the functional activity of the labial glands of *E. burchelli* therefore cannot be overlooked as a probable major factor underlying changes in the level of colony excitation and raiding activity during the late statary and entire nomadic phases. Depending upon the extent of raiding activity of the adult workers in *E. burchelli* colonies, there is a decided variance in the amount of food available at the onset and during the development of an all-worker brood. On the basis of SCHNEIRLA'S (1938, 1957) theoretical conclusions that the stimulative effect of the larval brood plays a major part in the continuation of the nomadic phase (once this phase is initiated through calow-brood stimulative effect) to its completion, these glands play an important part in the process. It is probable that the time at which they begin to secrete in the larvae has much to do with the onset and increase of feeding (brought about by an increased amount of raiding activity and an abundance of food) admitting an acceleration in growth which further increases the brood stimulative effect. Relative differences in their function may be considered a factor in the differential growth rate of the larvae and more specifically of larval structures such as the leg discs, as influenced by characteristic differences in the capacity of the larvae for feeding.

The first appearance of the imaginal leg discs corresponds significantly with the time at which the labial glands evidently become functional in larvae of the respective different size groups, as reported in terms of the 'phase-day' age. This is evidently a relatively strict correspondence, beginning with the first appearance of leg-disc development in the largest larvae of the series on the last statary day, when only these larvae have

functional labial glands. SCHNEIRLA's (1949, 1952) field investigations show that at this time the general level of raiding activity of the colony is still low although somewhat increased over preceeding days, and consequently the amount of food available in the bivouac is considerably less than in the nomadic phase. But when the smallest larvae begin to develop leg discs about the eighth nomadic day, all larvae of the developing *burchelli* brood have functional labial glands, raiding activity is high and the amount of food being brought into the colony is greater now than at any other time in the nomadic phase of activity.

It has been ascertained that during larval development in holometabolous insects, the growth rate and extent of development of the imaginal leg discs is dependent in part upon certain external factors (BODENSTEIN, 1939, 1941 and 1953). Among the most important of these factors are the relative amounts of available food, oxygen supply and the temperature of the environment. It therefore may be of some importance in considering the results of the present investigation, to review the afore-mentioned experimental evidence. It is apparent from experimental studies, that unless certain external requirements are present at a critical time (which is probably specific for each species, and perhaps for each structure), the expression of the potencies of these imaginal structures will be altered in some way (BODENSTEIN, 1939 and 1953, JU-CHI and YU-LIN, 1936; KAJI and OGAKI, 1953, and SHULL, 1937).

In view of these considerations, it is important to note that SCHNEIRLA *et al.* (1954) have found the army ant bivouac, or temporary nest of the nomadic phase, a relatively stable environment for the larval brood, leveling off environmental extremes such as lower nocturnal temperatures which might retard brood development. It also appears significant that, as these investigators report, the highest temperatures of the bivouac (ca. 29-30° C.) are maintained near its center, and more specifically, as JACKSON (1957) has subsequently found, a temperature gradient typically exists in the bivouac with its peak in the central area. Furthermore, a gradient normally exists in the distribution of larvae in the bivouac (SCHNEIRLA, 1938; SCHNEIRLA and BROWN, 1950) with the smallest larvae held centrally and the largest peripherally. In view of these facts, it is apparent that the differential microclimate typically operating for the different size-groups of the brood population is adequate to support the respectively different rates of development it was found characteristic of them. In other words, the smallest larvae, which evidently have the fastest rate of larval development, are usually located near the center of the bivouac where the highest temperatures prevail; the largest larvae, evidently with the slowest growth rate, are located marginally where the lowest bivouac temperatures prevail during the nomadic phase.

It is probable that differences in function of the labial glands depend upon their histologically different conditions in the brood population though larval development, as indicated in this study. Also, at different developmental stages other conditions governing food-intake may

account to an important extent for the fact that a differential growth rate seems to prevail among the larvae. The above ecological considerations suggest that once the smallest *Eciton burchelli* larvae are capable of feeding, situated in a higher temperature, they are relatively more active and consume more food in relation to their body size than do larger larvae. The existence of a differential growth rate of structure such as the leg discs in the polymorphic size-groups of *burchelli* larvae is consistent with the results of experimental studies of caste determination in the social insects. Such studies reveal that clues to the underlying mechanism of polymorphism point to the critical role of size and volume of larvae and the relative size and degree of development of structures such as the imaginal leg discs and wing buds at the time of pupation (BRIAN, 1951, 1952).

### SUMMARY AND CONCLUSIONS

1. The study of external and internal anatomy among larvae in the large polymorphic all-worker broods of *Eciton burchelli* indicates that although there are no identifiable qualitative differences among the larvae of any one brood sample in their general or detailed structure, there are consistent differences within any brood series as to the time of appearance of both general and detailed structural changes, as well as differences in relative growth rate through the polymorphic brood populations.

2. Caste differences are found for the time of appearance of both external structures such as mouth parts, antennal discs, imaginal leg discs and gonopodal discs and internal structures such as the alimentary canal, the Malpighian tubules, the central and stomatogastric nervous systems, the corpora allata, the labial glands, dorsal vessel, ovaries and fat tissue. These studies were carried out analytically in some detail for the leg discs among external structures and for the labial glands among internal structures.

3. Detailed anatomical and histological studies of the 'synthetic-series' of specimens representing brood samples of different colonies at intervals through the nomadic phase indicate that no one characteristic of external or internal structure can be used to distinguish larvae occupying different positions in the polymorphic series. Rather, in a brood sample taken at any one time in the nomadic phase, a graduated series of measurements is obtained with respect to size and degree of development of any external or internal structure. Furthermore, in samples taken at successively different times, an overlapping of the respective graduated series of measurements is obtained.

4. From these findings it is concluded that the chief differences to be found in a brood cross-section taken at any one time lie in the relative development of individuals through the series, with individuals of the largest overall size most advanced, those of the smallest overall size least advanced, and individuals of intermediate size correspondingly advanced.



Accordingly, external structural changes in certain cuticular modifications in mouth parts, and in the leg discs, and internal changes as in the labial, glands, appear first (*i.e.*, at an earlier 'phase-day') in the larvae of greatest overall size, next in larvae of intermediate size, and last in larvae of the smallest size.

5. The significance of the developmental status of labial-gland structures among of the polymorphic series, in relation to the differential growth rate of structures such as the imaginal discs, is considered in view of inferences as to functional changes in the light of previous studies of insect polymorphism.

Evidence from a detailed study of the development of the leg discs and of the labial glands indicates that these structures develop at the slowest rate in the largest larvae, at a somewhat faster rate in the intermediate larvae, and at the fastest rate in the smallest larvae. Present evidence indicates that, as TAFURI found in the larval brood of *Eciton hamatum*, the HUXLEY allometry formula may also apply to the larval brood of *Eciton burchelli*.

6. This evidence is interpreted as supporting the hypothesis that the first-laid eggs in any one normal (*i.e.*, all-worker) brood of *Eciton burchelli* are first to hatch and at any one time thereafter are most advanced in their development, the last-laid eggs are last to hatch and at any one time thereafter are least advanced in their development, with eggs laid at intermediate times correspondingly differentiated according to their respective times of appearance in the colony. It is also concluded that, by virtue of differential growth rates in the brood, the time differential at egg-laying is considerably reduced at larval maturity, in the attainment of this stage by the largest and by the respectively smaller members of the polymorphic brood series of *Eciton burchelli*.

7. Evidence from a detailed study of the developmental history of the labial glands in this investigation, considered in its relevance for salivary-gland and spin-gland functions, is found to support conclusions made by SCHNEIRLA from his investigations with respect to the significant role of stimulative and trophic properties of the larval brood for colony behavior.

### Résumé.

L'étude de l'anatomie, interne et externe, des larves d'un couvain polymorphe "all-worker" d'*Eciton burchelli* indique que, malgré le manque de différences significatives entre les structures globales ou partielles des individus appartenant aux divers groupes polymorphes, il existe des différences importantes dans la courbe de croissance parmi les individus des populations polymorphes. Des différences dues à la caste se manifestent lors de l'apparition des structures externes telles que les pièces buccales et les disques imaginaires des antennes, des pattes et des gonopodes. Des différences se manifestent également par des structures internes telles

que le tube digestif, les tubes de Malpighi, le système nerveux, les glandes labiales par exemple. En considérant une série complète du couvain entier prise à n'importe quel moment de la phase de développement, on a trouvé que les individus les plus gros étaient les plus avancés, ceux de volume moyen étaient moins avancés, et ceux de petit volume étaient les moins avancés.

Les résultats d'une étude détaillée du développement des disques imaginaires des pattes et des changements cytologiques se produisant dans les glandes labiales indiquent que les structures se développent le plus lentement dans les larves les plus grosses, un peu plus rapidement dans les larves de volume intermédiaire et le plus rapidement dans les larves les plus petites.

Les résultats d'une étude détaillée de l'ontogenèse des glandes labiales, considérées en rapport avec leurs fonctions de glandes salivaires et de glandes séricigènes, confirment les conclusions de SCHNEIRLA acquises au cours d'enquêtes antérieures au sujet du rôle important des propriétés stimulantes et trophiques du couvain larvaire dans le comportement global de la colonie.

### *Zusammenfassung.*

Untersuchungen der inneren und äusseren Anatomie von polymorphen "All-worker" Larven des *Eciton burchelli* Stammes zeigen keine erkennbaren Unterschiede qualitativer Art in der allgemeinen oder Einzelstruktur zwischen den verschiedenen Grössenklassen, hingegen konstante Unterschiede in der relative Wachstumsgeschwindigkeit.

Zur Zeit des Auftretens äusserer Strukturen wie Mundteile, Antennensprossen (scheiben) und imaginaerer Beinsprossen (scheiben), ebenso innerer Strukturen wie Labialdrüsen weisen die Gruppen Unterschiede auf.

Betrachtung einer gesamten Zucht zu einem beliebigen Zeitpunkt innerhalb der Entwicklungsphase zeigte, dass Individuen der höchststen Grössenklasse am Weitesten fortgeschritten waren, Individuen von mittlerer Grösse etwas weniger entwickelt und solche von der geringsten Gesamtgrösse den geringsten Fortschritt aufwiesen.

Einzeluntersuchungen über die Entwicklung imaginärer Beinknospen und über die cytologischen Veränderungen in den Labialdrüsen zeigen, dass diese Strukturen sich am langsamsten in den grössten Larven entwickeln, etwas schneller in der mittleren Grössenklasse und am raschesten in den kleinsten Larven.

Im Rahmen dieser Arbeit wurde eine Untersuchung der Entwicklungsgeschichte der Labialdrüsen in Bezug auf ihre Bedeutung für Speicheldrüsen und Spinndrüsenfunktionen durchgeführt, es zeigte sich, dass von SCHNEIRLA auf Grund früherer Untersuchungen gezogene Schlüsse, die bedeutsame Rolle der stimulierenden und trophischen Fähigkeiten der Larvenzucht für das Kolonieverhalb betreffen, bestätigt werden können.

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