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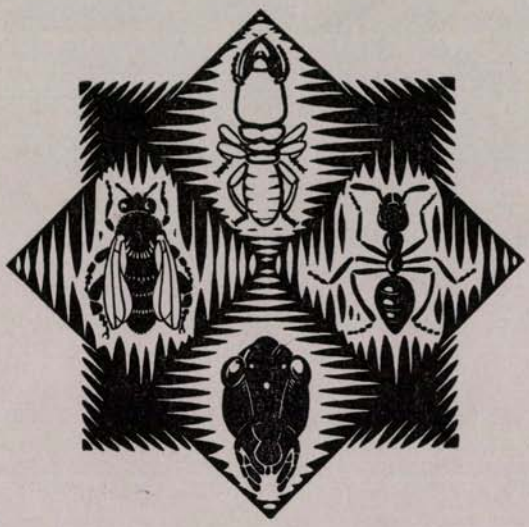

105, Bd RASPAIL
PARIS - 6e

NOTES ET COMMUNICATIONS

FURTHER WORK ON CASTE-DETERMINATION IN *MYRMICA*

by M.-V. Brian

Since a note was published in *Experienta* (Volume 7, page 182), the study of caste-determination in this laboratory has made some progress and produced some interesting results. By considering the imaginal rudiments in the larva, a number of problems that resisted rational analysis when only two variables, weight and time, were available, have now been solved.

Perhaps it would be best, first to recount the general sequence of imaginal development from the beginning of the final larval instar onwards. The brain of the larva moves gradually from the head into the prothorax. This is accompanied, and perhaps caused by the elongation of the imaginal antennary buds which lie in the head just in front of the brain. By the time of hibernation, the largest larvae have about 0,7 of the brain in the prothorax ; in smaller ones the brain is not so far out, and in the smallest, which only entered the instar just before the winter, the brain is still entirely in the head. In post-hibernation growth the movement of the brain is resumed, and the moment when it has entirely entered the prothorax is an important stage in development : it is followed by the segmentation of the legs (for convenience, the imaginal limb and wing buds will henceforth be referred to as legs and wings).

Hitherto, these buds have been involuting and enlarging, and have attained a subspherical form, but after the entry of the brain a slight elongation produces an elliptical form as seen through the larval cuticle. This elongation heralds division into two parts, a smaller basal, the femur, and a larger distal, the tibia and tarsus.

Shortly afterwards a small ring is split off the base of this distal segment — later to form the distal spur-carrying part of the tibia. The rest is the tarsus, the segmentation of which follows. After this comes a phase of expansion, beginning at the head where the enlarging antennae and mouth parts of the adult come to occupy the entire head and prevent continued feeding. The leg and wing buds elongate, bursting their sheaths and expanding into a lymph space formed between the larval and the new adult cuticle. The leg expansion involves a remarkable lateral movement that produces the long femur and tibia folded and lying side by side ; the tarsus alone of the leg segments appears to have room to expand in the anterior-posterior axis of the animal. The trochanter is formed from the base of the leg-sheath, and the coxa is carved out of the body-wall of the larva. Defecation follows, but the subsequent events are not at present of concern as the form of the adult is already fully-defined.

The transposition of the brain and the development of the legs have been used to chart the development of the larva, as they can after some practice be conveniently watched through the cuticle without any detrimental effect on the larva. Unfortunately the ovary is completely obscured by fat-body, and its changes have to be inferred by examination of equivalent fixed specimens. It first shows indications of splitting into ovarioles (in the queen organism) at the time when two well-defined leg segments are present. The time schedule of development at 25° C and optimal feeding, of a large hibernated larva (2,4 mg.) follows :

Day 0 0,7 of brain in prothorax ;
» 3 all of brain in prothorax ;
» 4 leg two segmented ;
» 6 leg three segmented ;
» 8 legs beginning to expand ;
» 9 legs and wings fully expanded ;
» 10 defecation.

Thus the first sign of a difference in form between queen and worker yielding larvae occurs about the fifth to sixth day when the ovary either splits into ovarioles or does not, as the case may be. At this stage the weight usually lies between 6.0 and 6.5 mg., and because the study of growth curves showed that workers never exceeded this weight, and since starvation of larvae 6.5-7.0 mg. in weight yielded mixtures of intercastes and queens whereas the

starvation of larger ones yielded queens, it was concluded that this visible differentiation marked the beginning of path divergence between queen and worker organisms (see the earlier account for details).

However, it has now been found that a divergence of *shape* precedes this divergence of *form*. This was discovered by studying the growth of wing and leg buds in a series of individual larvae of differing initial sizes. From this it appeared that the wing area of workers never exceeded four units whereas that of queens went up to 50 units. Wing area is also closely correlated with body weight, and a wing of four units was normally achieved by large queen-producing larvae after only two days culture when their weight was little more than 3.5 mg., and when the brain was not quite fully (0.9) in the prothorax. Nevertheless, this condition although in different individuals it may be reached at different times and at different sizes appears to be the earliest sign of path-divergence and may be the point of determination. Provisionally then it appears that if a larva contains wings that exceed four units in area when the brain is 0.9 in the prothorax it takes the queen path, if not, such wings as it has cease to grow and it becomes a worker. Larger hibernating larvae tend to achieve this more often than smaller ones in spite of the fact that they begin at a later stage of development. Hence shape dichotomy can be detected before the segmentation of the imaginal rudiments.

The specific growth rate of the queen-path larva is maintained for four or five days after « determination », but evidence at present shows that of the worker-path larva is reduced somewhat.

This would account for the small but definite gap (0.5 to 1.0 mg.) between the weight of the smallest queen and the largest worker in this species.

Further insight into the processes at work, may be obtained by considering the effects of starvation of larvae at different stages. Starvation between hibernation and full brain tranposition reduces the rate of brain movement by half, and all change is arrested when complete translocation has taken place. Larvae have been known to survive for 58 days in this condition, but the provision of only a milligram of protein causes rapid metamorphosis. On the other hand, starvation after the larva has passed this stage does not prevent metamorphosis, and has no effect on the rate of growth and development of the legs and the time of defecation. Before the legs are three-segmented, wing growth is arrested by starvation, afterwards

it is not. In males wing growth is always correlated with leg growth (and presumably in most winged insects). Thus aptery in ants, if these conclusions prove to apply to other species, would appear to result from a removal of the growth correlation or link between legs and wings, the wings growing only as the body as a whole grows until a late stage, the legs growing partly with the body and partly independently. Add to this a mechanism preventing further wing growth if a certain condition of size is not fulfilled when the brain enters the thorax, and the conditions for the production of a worker caste are complete.

Thus there seems to be good reason to consider that caste-determination and metamorphosis-determination occur very nearly at the same time, for independence of food-supply begins after the brain has entered the thorax, and is accompanied by a differentiation rather than a mere growth of the imaginal rudiments.

The adult forms emerging from these starved larvae are interesting. If starvation begins before three leg segments are apparent when the wing area is less than fifteen units, the adult is indistinguishable from a worker — and this in fact must have led to the earlier belief that determination took place just before the differentiation of the ovary. In fact, in the pupal stage the wings are small conical papillae, distinguishable from worker forms ; and pigmentation in the ocellar region (there are no lenses) is also perceptible for a brief time before it is obliterated by the general body infuscation. These starved forms are therefore strictly intercastes. Starvation at a later stage, when legs are three-segmented and the wings exceed twenty units in area produces perfect queens — the wings and legs have become growth-linked. It is only by starving in a very short period of development (wings 15 to 20 units) that the more grotesque types of intercaste can be produced. This corresponds with what has earlier been said.

In *Myrmica* the sterile caste is monomorphic, but these last observations suggest how a major worker and possibly a soldier caste could originate. Larvae that take the queen path might become arrested at the wing-15-units stage before the wing had become relinked to the leg growth system and whilst it was small enough not to show in the imago. So far some larvae starting at medium size (after winter) have, after taking the queen path almost ceased growing (and developing) in the two-segment leg stage. Up to the moment all have acquired another growth spurt that has taken them to full queen form. Will any fail to make this extra growth ?