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PAEDOGENESIS IN THE COLEOPTERA

By

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With 16 figures in the text.

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Paedogenesis in *Micromalthus*.

Introduction and History.

The general problem of bisexuality has some of its most interesting corollaries in those cases where the bisexual state is a cyclic one. The cyclic bisexuality may take any one of several different forms: for example, one familiar process involves the alternation of bisexual adults with a more or less long series of partheno-producing adult females as occurs in aphids, rotifers, cladocera, etc. Some of the most puzzling conditions, however, arise in those forms which combine parthenogenesis with paedogenesis. This type of reproductive behavior has been reported in a number of species in the dipteran family *Cecidomyidae*. It is therefore even more remarkable that a reproductive situation almost exactly similar in even minor details occurs in an insect remote from the midges, i. e., family *Micromalthidae*, order *Coleoptera*. It is my aim in this paper to outline with considerable detail the reproductive behavior of *Micromalthus debilis* (LE CONTE), also to describe and compare the reproductive anatomy of the various forms and finally to compare the situation with that found in the *Cecidomyidae*.

Occurrence. I have elsewhere noted the distribution of *Micromalthus* as including the states of New York, New Jersey, Michigan, Kentucky, Virginia[1], and I must now add Massachusetts, where I have recently found the animals in great abundance. The species inhabits many types of red rotten wood including pine, hemlock, chestnut, oak and probably others. The primary requirements seem to be that the wood be red rotten and fairly moist. Under these favorable conditions the animals bore long galleries and are able to live very satisfactorily in the center of a log which may exceed a foot in diameter. The genus *Micromalthus* stands alone and is represented only by the single species debilis, in fact, the species is alone in a monogeneric family. This taxonomic isolation is even more extensive for LE CONTE (8) was unable to definitely associate the *Micromalthidae* with any other coleopteran families.

The original account of paedogenesis in *Micromalthus* (1) met with a considerable amount of distrust among American entomologists, and although BARBER was correct in his conclusions in nearly every respect the slow acceptance of his work was undoubtedly due to the lack of illustrative evidence to support his contentions.

Methods.

Culturing. It is relatively easy to keep a stock of *Micromalthus* in the laboratory. Almost any device that will keep a log of red rotten wood sufficiently moist (but not saturated) proves satisfactory. The most convenient method for keeping such mass cultures is one devised by BARBER. Wooden boxes of various sizes are lined with plaster of paris and a glass lid tightly fitted to the top. The plaster serves admirably to hold the moisture for long periods. With such a simple moist chamber considerable quantities and sizable pieces of wood can be kept in what approximates the natural condition. I have kept such cultures for many months in a healthy state. This is, however, in no sense a method which allows individual examination. Indeed I have had unfortunate results with any method of individual culture, for invariably the larvae die. A recently devised method promises success for larvea have been kept for over a month in blocks of rotten wood completely coated with plaster of paris.

[1] Michigan, Kentucky, Virginia recorded by BARBER. 1913.

It is notable that in most instances where I have brought wood into the laboratory the great majority of forms develop into adult females, male producers and their male offspring. Such wood usually becomes drier and I believe, therefore, that relative dryness is an important factor associated with the development of these forms. On the contrary the thelytokous paedogenetic mother is frequently found in wood of relatively high moisture content. These facts obviously offer an experimental approach.

Fixation and Staining. I have employed a number of technical procedures during the course of this study, as fixatives BOUIN, B_{15} and KAHLE, as a stain for whole mounts of dissected ovaries and entire larvae, FEULGEN, which gives beautiful results, and carmine, which is somewhat less satisfactory. All sectioned material was stained with iron haematoxylin.

Life cicle in *Micromalthus.*

The life cycle of *Micromalthus* has been recorded by BARBER (1913 a, vide supra) and 1913 b (2) and briefly in a paper of my own (10) in which I reported haploidy in the male and recorded the course of the aberrant unipolar "division", of spermatogenesis. Much amplification is necessary beyond these brief accounts for no one of these papers has given a complete description or recorded the histology of the types. The accompanying chart (fig. 1) will serve to illustrate the main features of the cycle.

There are in this species four different kinds of reproductive females of which three are larvae. These four types I have designated as 1. an adult female, fig. 1 d; 2. a thelytokous (female producing) paedogenetic larva, fig. 1 b; 3. an arrhenotokous (male producing) paedogenetic larva, fig. 1 e; 4. a type intermediate between 2 and 3 that is an amphiterotokous (male and female producing) paedogenetic larva (newly reported in this paper), fig. 1 c. An adult male form, fig. 1 g makes a total of 5 reproductive forms in this single species.

A complete outline of the life cycle includes several other immature morphological types. 1. A hypermetamorphic larva (with well-formed legs having jointed tarsi) which develops from the eggs of the thelytokous paedogenetic female. This first stage larva completes its early development within the follicles of its paedogenetic mother (compare fig. 1 b and BARBER's photographs 1913 a plate 3) and at term is shed in a perfectly regular manner through the oviducts and genital aperture of the mother. 2. The first stage larva gives rise at a succeeding moult (probably the first) to a second stage larva which is similar in most details but lacks legs, fig. 1 a. Both of these larvae have large biting jaws and a chitinious anal armature. 3. A third distinct immature larval form is the male larva which hatches from an egg shed by the male producer (arrhenotokous paedogenetic mother). The young male is a short stubby form with stump-like legs and showing certain superficial resemblances to the curculionid larvae. 4. Two pupal forms male and female recognizably distinct, complete the list of morphological types.

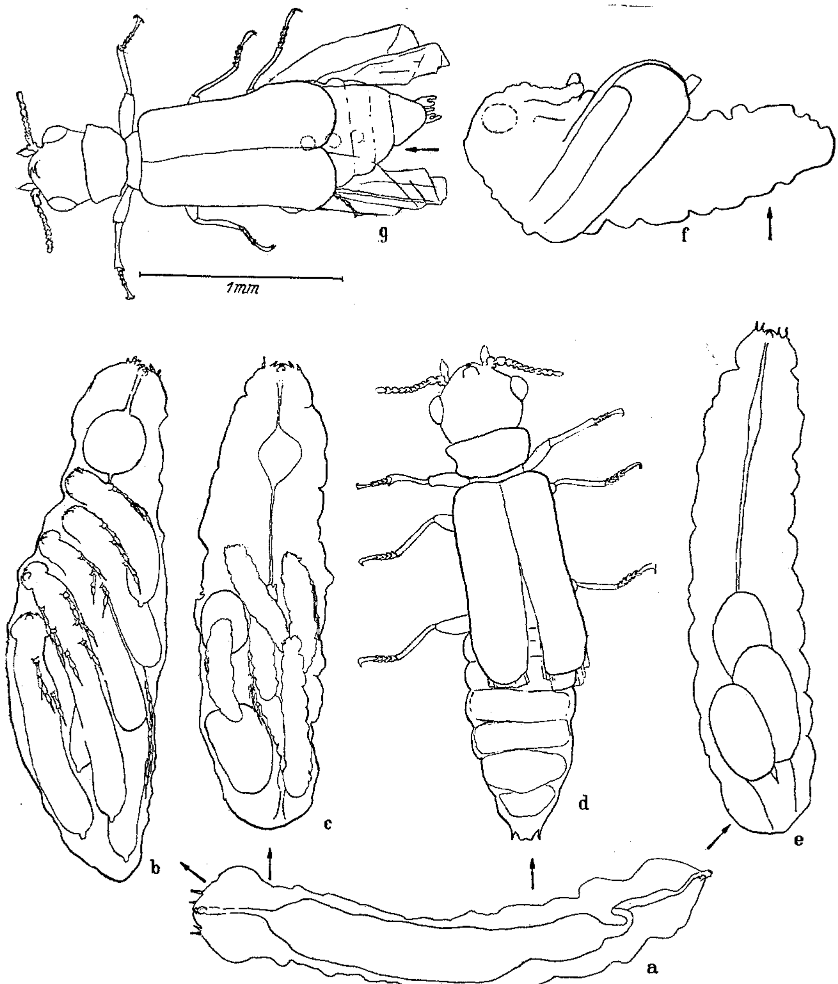


Fig. 1. Diagramatic representation of the essential features of the life cycle of *Micromalthus*; a pleuripot nt second stage larva which can develop into any one of the four reproductive types; b thelytokous paedogenetic female; c Amphiterotokous paedogenetic female; d adult female; e Arrhenotokous paedogenetic female; f pupal male; g male adult. All drawn to the same scale with the camera lucida.

The female reproductive types.

The adult female. According to Barber, the adult female is the primary migrant and functions in the establishment of new colonies. I cannot wholeheartedly subscribe to this notion since several considerations seem to argue against it. 1. The adult female has (even several days after eclosion) only two eggs anywhere near the mature stage and these never seem to lose a conspicuous germinal vesicle. 2. Isolations of adult females have failed to induce oviposition in any case. 3. I have never observed copulation of the adults and I do not find sperm in adult females that have been for some days with males although a spermatheca is present[1]. This last point is perhaps not a serious objection in view of the possibility of parthenogenesis. But the first objection carries much weight; it therefore appears that the first stage larva is the primary migratory form of the species. The question arises as to how early one may recognize the presumptive female adult in her development. Fig. 2 illustrates the female prepupa at approximately the first stage possible to recognize. Notable are the indications of segmentation into head, thorax and abdomen. I shall point out below how such a female may be recognized much earlier by inspection of the ovary. After flexion of the head and growth of the wings, the female pupa appears as fig. 9a.

Fig. 2. Early pupal or prepupal female in which indications of segmentation into head, thorax and abdomen are present. Length 2.8 mm.

The sexual adults mature normally only once each year in the vicinity of New York. They emerge quite usually (females about a week in advance of the males) during the second and third weeks in August. Adults may, however, be induced to mature in the laboratory in any month of the year by the proper adjustment of temperature and moisture conditions.

The thelytokous paedogenetic female. The three larval reproductive forms are indistinguishable until the middle of the penultimate instar at which time the thelytokous paedogenetic female can be identified by the presence of elongating eggs and early embryos. These eggs are visible through the integment and often the germinal vesicle is clearly visible. It is not, however, possible to distinguish all early thelytokous paedogenetic females this early since many cases occur in which fat bodies obscure the embryos.

During the last instar the larval young of the thelytokous mother grow rapidly and progressively distort the maternal body, fig. 3. Indeed

[1] Barber has repeatedly observed copulation and believes that the adult female is fertil. I have much respect for his observations and must attribute my inability to observe mating to some unknown factor. Notwithstanding the observations of Barber the evidence favors the conclusion that the adult female is rarely if ever functional.

movements of the offspring are easily seen as they move about within the body of the mother. The orientation of the embryos in the maternal ovary-brood sacs is interesting. They are always oriented with their anterior and posterior and likewise their dorsal ventral axes corresponding to the axes of the mother. The diagram in fig. 1b of the thelytokous paedogenetic female illustrates this correspondence very well (axial gradient relationship).

At term the first stage larvae are shed by their paedogenetic mother one by one, tail first, as BARBER described long ago (fig. 4). The process occupies from one to several hours depending upon the number of offspring developed within the mother. After devouring their mother these young, legged larvae burrow into the surrounding wood. The greater

Fig. 3. Thelytokous paedogenetic female stained entire with feulgen; the well developed young are deeply stained. Length 2.5 mm.

Fig. 4. Viviparous paedogenetic female giving birth to a first stage larva. Offspring are always born tail first and one after the other; they have no membrane investing them.

number of broods of these thelytokous paedogenetic larvae are formed in July, August and September, although they occur in smaller numbers during every month of the year excepting the coldest, December, January and February when, in my experience, no broods have been found. The number of first stage larvae which constitute a brood varies from as few as four to more than twenty. (Compare fig. 5 which shows a brood of 11 and a remnant of their mother.) Apparently the size of the brood is very much influenced by the environment because animals from the same region in a log usually produce about the same number of offspring.

Two morphological changes affect all three paedogenetic larvae at their last moult, 1. they lose their chitinous anal armature and 2. their jaws are considerably reduced in size.

The arrhenotokous paedogenetic female. The arrhenotokous paedogenetic female can be recognized in the penultimate instar by the rather vague criterion of a dense white color due to much fat. Moreover, the male producer can be identified in the last instar by her cylindrically shaped body and by the presence of marked segmental constrictions. In fig. 6 such a female is shown as she appears after staining entire with feulgen, two round male type eggs can be easily seen. The male producer generally sheds a single large egg (the potential male) early in July and four or five weeks elapse until eclosion of the male adult. The production of the male is an annual event normally occurring in August each year but males can be induced to develop in the laboratory at practically any season by merely keeping moist wood at room temperature. It is extraordinary that only one egg is shed of the several present in the ovary of

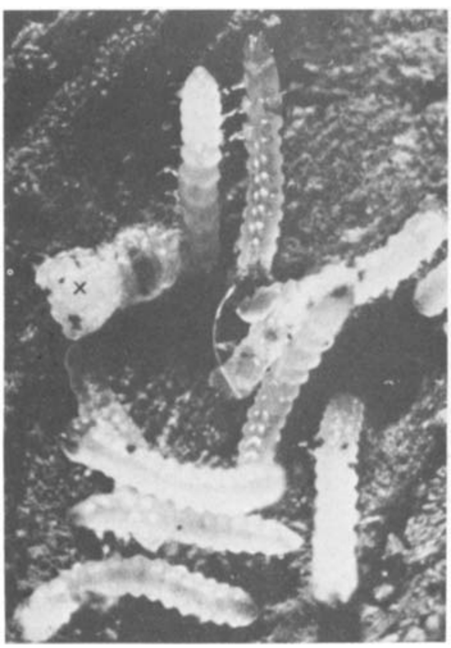


Fig. 5. A recently born family of eleven first stage larvae and a remnant of their viviparous, paedogenetic mother. Note the legs on the first stage larvae and that which remains of the mother at x.

Fig. 6. Lateral view of a male producing female stained entire by the feulgen technique. *n* ganglion; *e* large male type egg; *g* gut. This larva is 2.1 mm. long.

the male producer. In three exceptional cases I have discovered two eggs on the outside of the mother and have confirmed their origin from the mother larvae by finding two empty follicles on dissection. The male undergoes some development while still within the mother[1]. After emergence the egg (young male) remains adherent for two or three days to some part of the mother, fig. 7a, and finally inserts his head into his

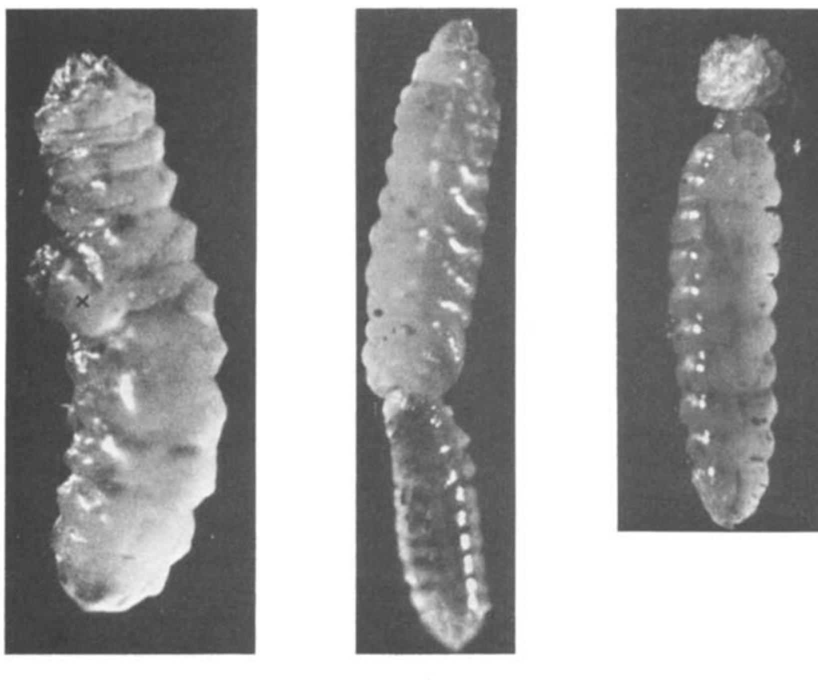


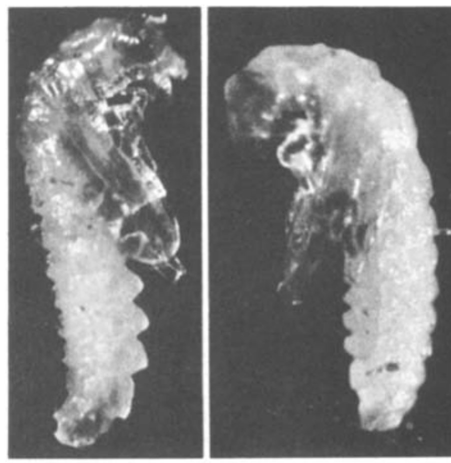
Fig. 7. Three stages in the development of the male; a the male adherant to the mother at x; b young male larva devouring his mother; c well grown male larva, mother almost completely eaten.

mother's genital aperture and feeds upon her, fig. 7b. A somewhat later stage, fig. 7c, shows only a remnant of the mother. In the course of a week of feeding, often less, the mother has been completely devoured and the male is nearly ready to pupate. Such a male, fig. 8, shows clear segmentation into head, thorax and abdomen. The length of time taken for development in all forms, excepting the male, is a remarkably long one. It is certainly several months at room temperature for all the female forms and even the relatively rapid development of the male requires from twenty to thirty days (from the shedding of the egg until eclosion).

[1] This matter needs more attention. I do not know precisely at what embryonic stage the male is shed; the oldest embryo I find within the maternal ovary is quite young (germ band stage).

The amphiterotokous larvae. Concern over the possibility of the existence of barren larvae described by Barber (1913b) led me after dissection to the discovery of a bivalent larval type previously classified as an immature male producer. Careful investigation now shows that these are not an nfrequent type for I have encountered many since their first discovery. It is significant that these amphiterotokous larvae first

Fig. 8.



a b

Fig. 9. Pupae in lateral view for comparison of the body form of the sexes. Abdominal sternites appear serrate in the female and papilliform in the male.

Fig. 8. Late larval male that has finished feeding. Note the conspicuous legs on the thorax.

appear in wood with well developed male larvae or male pupae. That is, they regularly follow the male producer by three or four weeks. Dissection has proven that they are, in fact, male producers which for some reason either shed no eggs or the shed egg has failed to develop and a new crop of eggs of the thelytokous type have budded from the ovary. Such bivalent paedogenetic larvae ultimately give birth to four or five first stage larvae similar at least morphologically to the offspring of the thelytokous larval mother. It is my opinion that it was these amphiterotokous larvae that Barber considered as barren. Fig. 1c was drawn from one of the bivalent paedogenetic larvae which had been stained entire with feulgen.

The male. Although the life history of the male has been discussed in connection with the male producer, the following summary will serve to consolidate the facts already presented. 1. The male is the sole offspring of a male producer; he originates from no other source. 2. One or several other male embryos may be present in the same mother — only the successful male, however, is deposited. 3. The male is haploid in both somatic and in spermatogonial cells. 4. The two divisions of spermatogenesis are a) an abortive unipolar first maturation division and b), a bipolar equational second maturation division. 5. During early development the male eats his mother, and although he develops from an egg of very different size and shape from those which give rise to females, and although his development is entirely different and the rate of his development is many times faster, nevertheless the male and female daults are closely similar in appearance. The male anp female pupae rea shown in fig. 9a and b. The male is slightly smaller on the average than the female and there is a marked difference between the sexes as regards the contour of the abdominal sternites, in the female the abdomen presents a serrate appearance, while in the male the sternites are more papilliform. Sections of the adult male abdomen show the histological nature of the three flask shaped glands peculiar to the male (fig. 10).

Fig. 10. A cross section of one of the three sternal glands of a late male pupa.

Internal reproductive anatomy and early differentiation of the ovary.

Internal changes in the ovaries first indicate the differences among the various reproductive forms; gross anatomical differences occur only later. The ovaries of the mature female types are very different, although differentiation is only gradually attained. All early female larvae (first stage) have an undifferentiated ovary of small size forty micra (longest dimension) and of nearly uniform histological structure. Each consists of a mass of small cells with relatively large nuclei and no discernible cell wall. This same condition obtains in the slightly larger ovaries of the early second stage feeding larvae in which the ovaries may measure one hundred and twenty micra in the longest dimension. From this indifferent state the ovary differentiates into one of the three following: 1. the small partially abortive ovary of the adult female containing rarely more than one sizable egg (one hundred and fifty micra), fig. 11b, 2. the ovary of the male producer with its relatively large eggs and with stout oviducts attached (six hundred micra), fig. 11c, or 3. the immense ovary brood chamber of the paedogenetic viviparous female (often over two thousand micra), fig. 11a.

The first steps in the differentiation of these young ovaries involves three well defined events: 1. the lobulation of the ovary, 2. the formation of cell clusters (early nurse cells), and 3. the enlargement of the presumptive egg cells. Lobulation sometimes occurs in ovaries as small as seventy micra in length and the enlargement of the egg cells may likewise

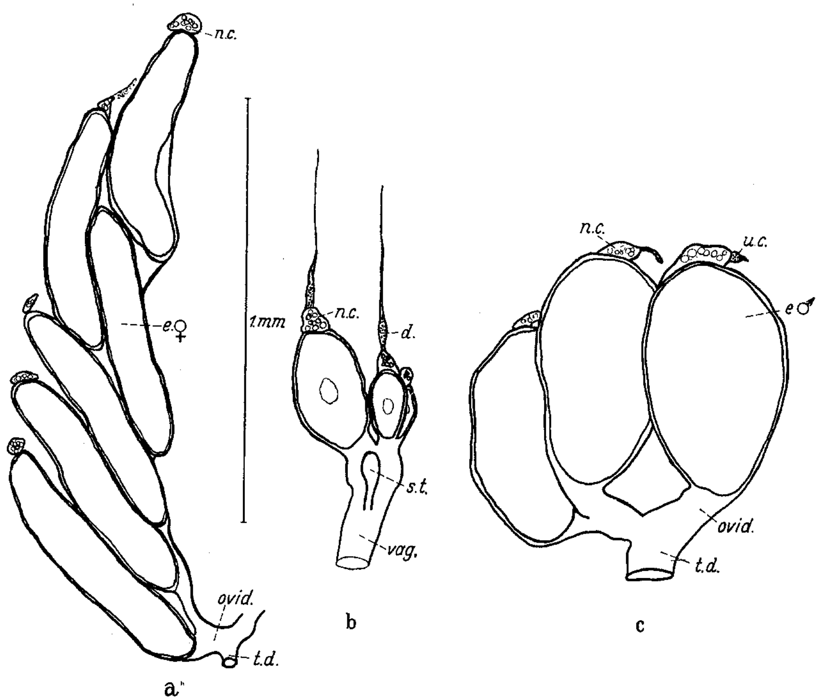
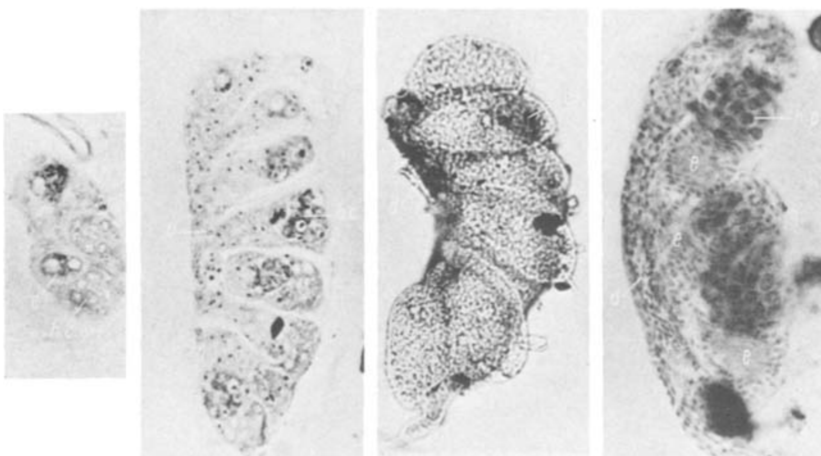


Fig. 11. Diagram of the reproductive apparatus of each of the three primary reproductive types in dorsal view. a the thelytokous paedogenetic female (only one of the two ovaries is drawn of the thelytokous female); b the adult female; c the male producer; *d* degenerate ovocytes; *f* follicle; *s. t.* spermatheca; *u.* uterus; *t. d.* terminal duct; *n. c.* nurse cells; *e.* egg; *ovid.* oviduct; *vag.* vagina; *u. c.* undifferentiated cells.

begin at this early stage. But although the ovary may show such differentiation when still so small, one can make no certain prediction of its fate until it has become two hundred and fifty micra in length. In general, one may presume that such small ovaries (seventy to one hundred micra) are 1. destined to become adult female ovaries if many lobes and few or no large cells are present, or 2. are destined to become ovaries of viviparous females if many lobes and many eggs are present, or again 3. are destined to become the ovaries of the male producer if few lobes and few eggs are present. Thus there is considerable probability that the eighty micra ovary, fig. 12a, is from a very young arrhenotokous paedogenetic female because of the few lobes (seven or eight) and the relatively few enlarging eggs. A somewhat larger ovary (one hundred and eighty micra) is almost certainly an early thelytokous paedogenetic female for the ovary shows an oviduct anlagen and is distinctly lobulated into many lobes, each of which contains a group of nurse cells and one or more enlarging eggs, fig. 12b. By the time an ovary has grown to two hundred and fifty micra in length, its fate is unequivocal. Fig. 12d illustrates the smallest ovary yet found, which is certainly from an arrhenotokous paedogenetic female. The ovary contains three enlarging eggs, each associated with a cluster of nurse cells. Only three lobes are present, therefore, in the ovary. That



a b c d

Fig. 12. Young ovaries of paedogenetic females. a Section of an ovary 80 μ long showing few lobes and few eggs (presumably a male producer); b Section of an ovary 180 μ long with marked lobulation and many eggs (doubtless an early thelytokous mother); c whole mount of a 250 μ ovary from a male producer, 3 eggs only; d whole mount of a 275 μ ovary of a thelytokous mother; *e* egg; *n. c.* nurse cells; *d* duct.

such ovaries may earlier have more lobes is indicated by the fact that in some young ovaries whole groups of cells become pycnotic and disappear. Fig. 12c illustrates similarly the smallest unequivocal thelytokous paedogenetic female ovary. In this case, however, the number of lobes is greater (fifteen) as indicated by many eggs and nurse cells. Both of these ovaries are two hundred and fifty micra in length, they possess a duct (or anlagen of a duct) and the enlarging egg cells are clearly surrounded by a layer of follicle cells.

Mature ovary — thelytokous paedogenetic female. The primary characteristic of the thelytokous ovary is the presence of many eggs, and attention has already been called to fig. 12b, which illustrates in all probability a very young ovary of this type, and to fig. 12d, which illustrates a thelytokous ovary of much larger size shortly before maturation. At the approximate time of maturation the eggs and follicles undergo extensive elongation. During early cleavage the eggs of the thelytokous paedogenetic ovary measure from four hundred and fifty to five hundred micra in length, and from this time forth they undergo steady development and growth until they are shed as fully formed first stage larvae. Each follicle, therefore, functions for a considerable period as a brood chamber for one embryo. The follicles become extremely long as the embryos grow for first stage larvae may measure two millimeters. At term the ovary fills the entire thorax and abdomen, and the young larvae are oriented with t heir major body axes corresponding to those of their mother. Each follicle is connected at its posterior end to a common short duct which leads to the outside (fig. 11c). There is no uterus, vagina or spermatheca. The first stage larvae are born tail first in the manner already described.

Mature ovaries of the male producer. The male producer gives rise to the male by haploid parthenogenesis (SCOTT, 1936). The mature ovaries (fig. 11b) are connected each to a large, short oviduct which in its turn leads into a common terminal duct ending at the large genital aperture. There is no differentiated uterus, vagina or spermatheca as in the adult female.

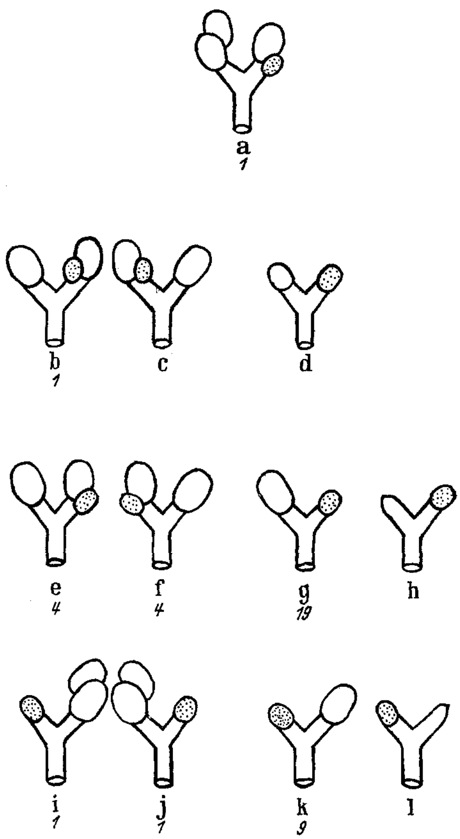


Fig. 13. Diagrams indicate the types of ovaries found in male producers that have shed one egg. Figures represent of each typ in forty females dissected with special reference to laterality. Further clarification in the text.

Male producers mature very few eggs (from one to five in my experience). From one lot of one hundred and eighty-six arrhenotokous females, the following tabulation resulted (Table 1).

Fig 13 illustrates the appearance of ovaries dissected from male producers that have shed the one functional egg. Ovaries which contain from one to four eggs are illustrated. A careful dissection of forty male producers has shown 1. that position

Table 1.

# of eggs both ovaries	# of larvae	%
1	2	1
2	133	71
3	43	23
4	8	4

does not determine which egg shall be discharged, 2. that the successful egg can be shed from either ovary[1], 3. that in cases where two eggs are present in one ovary either ma emerge. Small figures below the d~~y~~rawings of text figure indicate the number of cases in forty that each pattern occurred. It appears that a condition where one egg is present in each ovary is the most frequent one. Normally the arrhenotokous mother is eaten by the male which has emerged (fig. 7b). If this male

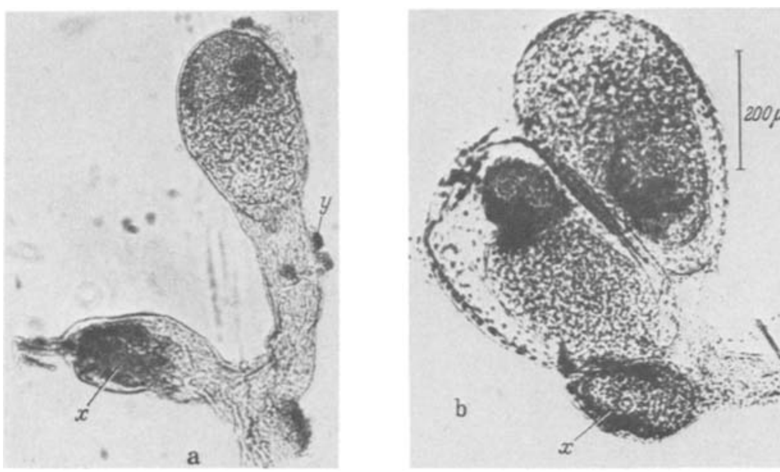


Fig. 14. Whole mounts of ovaries of male producing females stained with the feulgen technique. a an ovary which has shed one egg; b an ovary which has shed one egg and retained two. *X* empty follicle; *Y* undifferentiated cells.

dies it does not cause another egg to be laid but may allow the development of new eggs of the thelytokous type (cf. below). Thus the larval mother may become an amphiterotokous paedogenetic larva. Unshed eggs of the male producer undergo only a limited often very abnormal development (fig. 14a and b) before they are eaten together with the rest of the mother by the successful male.

Ovaries of the amphiterotokous female. Dissection of the mature amphiterotokous larvae reveals both large eggs (potential males) and elongate eggs or first stage larvae (fig. 15a). This adds another form to the small list of animals whose eggs show a marked sexual dimorphism (rotifers, phylloxerans and dinophilus). All ovaries from these bivalent paedogenetic mothers are first like those of an ordinary male producer[2]; they usually consist at this early period of two large eggs (one in each ovary). Each egg is connected by a short stout oviduct to a common genital duct. The thelytokous eggs always develop after the large eggs

[1] This fact is also indicated by those rare cases in which two eggs are shed.

[2] This is probably a superficial parallelism. It is considered in some detail in the following discussion.

have become mature. Thus in fig. 15b, there are many small sprouting thelytokous eggs attached to the follicle wall of a large egg. The point of origin of the elongate eggs lies in the little patches of undifferentiated cells which are present near the junction of the oviducts in the amphitero tokous female and along the sides of the egg follicles (fig. 14a at γ). Most commonly five first stage larvae are shed by such paedogenetic mothers. The fate of the eggs is variable: 1. they are only very rarely shed — this means that male producers that have shed their usual one of two or three eggs are able to turn about and become functional paedogenetic mothers of the viviparous type if the male does not develop after birth or if for some reason no male is shed; 2. the retained eggs (potential male type) may or may not begin to develop, in fact, one egg which has begun development and one which has not may be found in the same mother larvae. When development does occur in this egg it never progresses far and is frequently abnormal. In any case degeneration soon sets in[1].

The ovary of the pupal and adult females. The earliest pupal female has an extremely large ovary with six or eight lobes, each lobe containing hundreds of small cells with relatively large nuclei and chromatin in synezisis. This is the time of maximum size of this type of ovary (three hundred and twenty-five micra greatest length) yet no enlarging egg cells of any considerable size are evident, although in paedogenetic

Fig. 15. Ovaries of Amphiterotokous females (a above). Whole mount of an ovary which shows two well developed female embryos and two degenerate male embryos (b below). Whole mount of an earlier stage showing one degenerating male embryo and several young budding eggs which will become females. Both ovaries stained with feulgen; *e* egg; *n. c.* nurse cells.

[1] No cytological counts are available in these degenerating eggs which attest their haploid nature and presumptive maleness but the eggs in every way resemble those of the male producer previously shown to be haploid. Scott (ibid.).

ovaries of the same size eggs are conspicuous. When the wings have grown and eyes have turned yellow, the more anterior lobes begin to retrograde, and in the most posterior lobe adjacent to the oviduct one egg (sometimes two) begins to enlarge. Such an ovary from a pupal female with the more anterior portions degenerating is shown in fig. 16a. It measures two hundred and twenty-eight micra. The degeneration of the anterior lobes

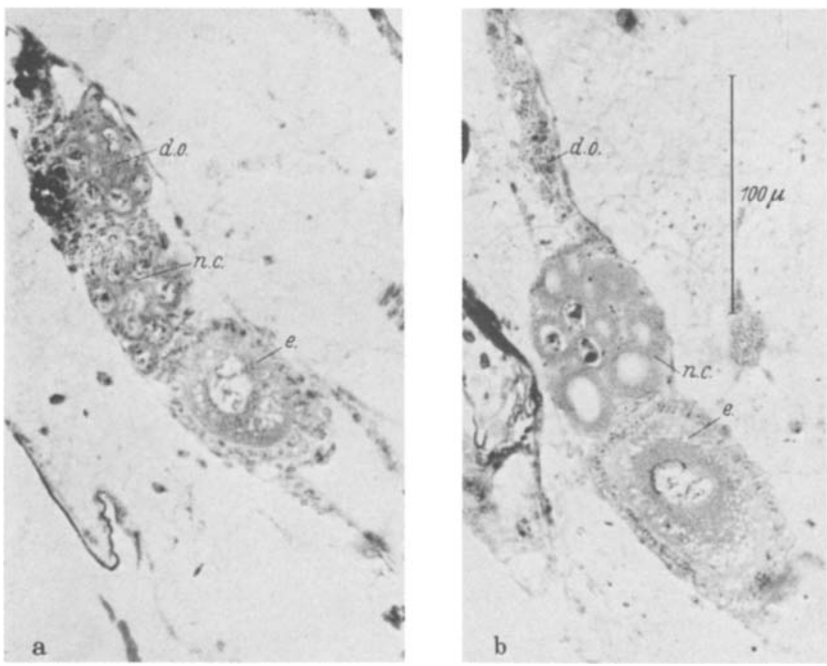


Fig. 16. a Section of the ovary of the pupal female showing a conspicuous mass of partially degenerate ovocytes; b Section of the ovary of the adult female showing further degeneration of the ovocytes. The egg still possesses a mature germinal vessicle. *n. c.* nurse cells; *d. o.* degenerate ovocytes; *g. v.* germinal vessicle.

of the ovary continues so that the major part of the adult female ovary measures only one hundred and fifty micra. The degenerate anterior portion is of an equal length (fig. 16b). The adult female reproductive structures, therefore, consist of 1. two ovaries, each containing a single immature egg or, rarely, two such eggs, and at the anterior end of each egg a mass of large nurse cells, 2. a degenerate strand of cells anterior to the nurse cells, 3. two oviducts, 4. a uterus, 5. a vagina, 6. a spermatheca.

Discussion.

Paedogenesis as a feature of cyclic sexuality has been known in insects for nearly three quarters of a century, yet only recently has a promising experimental approach to its problems been made. HARRIS (6, 7), SPRINGER (11), GABRITCHEWSKY (4, 5), and especially ULRICH (12) have indicated the relationship of environment to the determination of reproductive form. They have, however, studied only the paedogenetic *Diptera* of the single family *Cecidomyidae*. My work following that of BARBER has disclosed that the paedogenetic beetle *Micromalthus* shows a remarkably close parallelism of forms with those found in the fly *Oligarces*. This close similarity between two widely separate *orders* of insects leads one to the general conclusion that the evolution of paedogenesis most successfully follows a very definite pattern.

The recent work of HANS ULRICH forms a point of departure for the comparison of forms in *Micromalthus* and *Oligarces*. The accompanying table (Table 2) indicates the amazing correspondence of forms in these two species.

Table 2.

Micromalthus	*Oligarces*
1. new born indeterminate first stage larva,	1. frisch geschlüpfte undeterminierte Tochterlarve,
2. thelytokous paedogenetic mother larva,	2. thelytok pädogenetische Weibchen-Mütter,
3. arrhenotokous paedogenetic mother (male producer),	3. arrhenotoke pädogenetische Männchen-Mütter,
4. amphiterotokous paedogenetic mother,	4. amphoterotoke pädogenetische Männchen-Weibchen-Mütter,
5. female pupa larva,	5. weibliche J.-Larve,
6. female pupa,	6. weibliche Verpuppung,
7. female imago,	7. weibliche Imago,
8. male pupa larva,	8. männliche J.-Larve,
9. male pupa,	9. männliche Verpuppung,
10. male imago.	10. männliche Imago.

Such a parallelism involving three female reproductive forms which are paedogenetic as well as the expected male and female adults must have some general significance when one considers that paedogenesis is not a common phenomenon and the flies and beetles can in no sense be considered related forms. It should be *emphatically stated* that paedogenesis has become the all important method of reproduction in both species. Destruction of the paedogenetic mode of reproduction would result in destruction of the species. Judging from the nature of paedogenesis in these two cases, it would appear that it is successfully established with the following results: 1. The fertility of the adults is either considerably diminished or the adults are completely eliminated as a successful reproductive type. 2. Larval types develop which combine parthenogenesis with paedogenesis. These become the important forms for the perpetuation of the species. 3. The adult male is regularly derived from a paedogenetic mother. 4. There is a tendency toward the separation of male production from the production of females in the paedogenetic forms.

Each of these four points can be profitably considered in some greater detail. Whatever has caused the limited reproductivity of the adults in these paedogenetic forms is not apparent. It may perhaps be expected that the adults will eventually disappear. This is more apparent since Ulrich has shown that the paedogenetic mode of reproduction can continue indefinitely. A novel viewpoint would be to look upon paedogenesis as a compensating reaction resulting from the diminished reproductivity of the adult female whatever the cause may be of such non-productivity. Such an explanation serves to some extent to relate and to explain the first two general conclusions enumerated above.

It seems clear that with the adoption of the paedogenetic mode of reproduction there has developed a tendency towards the separation of male production from female production. This is perhaps *only* a tendency in *Oligarces,* but it is an accomplished fact in *Micromalthus.* I believe that the amphiterotokous mothers are not strictly comparable in these two paedogenetic species in view of several well defined differences which I summarize in the following tabulation:

Table 3.

Micromalthus	*Oligarces*
1. The amphiterotokous mothers are relatively rare,	1. The amphiterotokous mothers are a large group,
2. The amphiterotokous mothers are first determined as male producers.	2. The amphiterotokous mothers develop male and female producing eggs simultaneously,
3. The male embryo is rarely or never shed and never develops far in amphiterotokous mothers,	3. The male larva is shed and develops to maturity,
4. The embryo is probably haploid and male as in male producers.	4. The male is diploid.

Considered logically it seems most probable that when paedogenesis first began to develop in these insects the earliest paedogenetic forms were of the amphiterotokous type. The condition now obtaining in *Micromalthus* is doubtless the more highly evolved since it involves a complete separation of male production from female production in the paedogenetic larvae. Only exceptionally is a paedogenetic mother with a mixed brood formed from an already determined male producer. Ulrich contends that a sex determination process in the eggs is what determines the type of paedogenetic mother in *Oligarces.* In that species the bivalent larvae form a large group and may be arranged in a series. At one end of the series are mothers which contain one male and many females, at the other end of the series one female and many males. The former obviously differ but little from the thelytokous paedogenetic mothers, the latter resemble closely arrhenotokous paedogenetic mothers. Thus in *Oligarces* the primary bivalent type is still an important one. The amphiterotokous paedogenetic larvae of *Micromalthus* are, on the contrary, not comparable with the primary bivalent larva, but are a differentiated male producing type which in extraordinary conditions develops a few female larvae.

With these considerations in mind it is possible to construct a reasonable theory which will explain why there has been a tendency during evolution to separate the process of male production from that of female production in the paedogenetic larvae. This tendency is, I believe, related to the following two conclusions: 1. The adults (and therefore the male producer) are of little value to the species (either *Micromalthus* or *Oligarces*)[1] and 2. the type of most value would be a purely thelytokous paedogenetic female whose offspring were *all* of similar type. Such a female would waste no reproductive energy by producing adults. Selection could not effectively operate upon a pleuripotent paedogenetic type towards the elimination of adults, but if the process of male production and adult female production should be concentrated in special types of mothers, then the elimination of these by natural selection would purge the species of these useless forms. If this reasoning is correct, then it serves as an explanation of the apparent tendency to separate male production from female production in paedogenesis. It likewise explains why males originate from paedogenetic mothers. The separation is an accomplished fact in *Micromalthus* and under way in *Oligarces*.

Sex determination and Paedogenesis. While little is known concerning sex determination in the paedogenetic insects, still some consideration of the problem is of interest. No simple chromosome mechanism will serve as a physical basis for sex determination in *Micromalthus* and *Oligarces*. Moreover, the mechanism in the paedogenetic diptera is unquestionably basically different from that which serves for *Micromalthus* where haploid parthenogenesis is involved. If any chromosome mechanism serves in this paedogenetic beetle, it may be such a one as operates in the parasitic wasp Habrobracon juglandis (WHITING) 1933. On this basis all female types would possess two sex chromosomes, one different from the other; all females are thus XY; haploid males arising only from XY paedogenetic male producers would be either X or Y. Paedogenetic females which arise by diploid parthenogenesis would be

[1] All workers on the paedogenetic *Cecidomyidae* appear uncertain about the developmental potentialities of the eggs of the adult female. Can they give rise to males? Are they facultatively parthenogenetic? In *Miastor*, at least, they must be fertilized, according to GABRITCHEWSKY.

consistently XY. I mention WHITING's theory as the most promising answer to the old question — why is a haploid animal always a male[1]? It is apparent from the work of REITBERGER (1934) that an extensive chromosome elimination occurs in the early cleavages of *Miastor* and *Oligarces*. Any consideration of sex determination in the paedogenetic diptera must, therefore, await completion of these studies[2].

Summary.

1. The Coleopteran *Micromalthus debilis* LE CONTE is remarkable for the fact that there are in the species five mature reproductive forms. These are 1. an adult female, 2. a thelytokous paedogenetic female, 3. an arrhenotokous paedogenetic female, 4. an amphiterotokous paedogenetic female and 5. an adult male.

2. The adult is probably sterile, the thelytokous paedogenetic female is the essential reproductive type. She gives rise by parthenogenesis and vivipary to a sizable brood of indeterminate larvae. The arrhenotokous paedogenetic female matures a number of eggs of the potential male type only one of which is shed. The haploid male arises from no other source. The amphiterotokous paedogenetic female has proven tobe essentially a male producer in which the development of the male is arrested and female producing eggs develop secondarily.

3. In the text the development of the very different ovaries of the several female types is outlined and illustrated.

4. In the paedogenetic *Diptera, Oligarces* and *Miastor* the same types of reproductive forms as listed for *Micromalthus* occur. This has led to the conclusion that the development of paedogenesis is related to the following conditions: 1. The fertility of the adults is reduced or eliminated. 2. Larval types develop which combine paedogenesis and parthenogenesis. 3. The adult male is regularly derived from a paedogenetic mother. 4. There is a tendency towards the separation of male production from female production in the paedogenetic forms.

5. The hypothesis that paedogenesis developed as a compensating factor in response to the deminishing fertility of the adult female serves to explain several features of these peculiar life histories.

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[1] FANKHAUSER's recent "female" salamander raised from an egg fragment and posessing only the sperm nucleus should be recorded here (3).

[2] Altho the recent paper of Z. KRACZKIEWICZ (LA CELLULE 46) sheds no light upon the mechanism of Sex determination in the paedogenetic fly MIASTOR, it does relate some interesting chromosome conditions. The somatic cells of the male have 7 chromosomes while the somatic cells of the female have 12. The germinal cells of both sexes have 48 chromosomes. In MIASTOR, therefore, the determination of sex is complicated by a chromosome elimination process.

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