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# The life cycle of *Micromalthus debilis* LeConte (1878) (Coleoptera: Archostemata: Micromalthidae): historical review and evolutionary perspective

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## Abstract

*Micromalthus debilis* LeConte (1878), has one of the most bizarre life cycles of any metazoan. Reproduction is typically by thelytokous, viviparous, larviform females, but there is also a rare arrhenotokous phase. The active first-instar (triungulin) larva develops into a legless, feeding (cerambycoid) larva. This form either pupates, leading to a diploid adult female, or develops into any of three subsequent types of reproductive paedogenetic forms: (1) a thelytokous female that produces triungulins via viviparity; (2) an arrhenotokous female that produces a single egg that develops into the short-legged (curculionoid) larva, eventually devouring its mother and becoming a haploid adult male; or (3) an amphitokous female that can follow either of the two above reproductive pathways. We speculate that *Micromalthus* is dependent on maternally transmitted bacteria for the ability to digest rotting wood, and that these bacteria are senescent in males, causing males to be obligately cannibalistic. Obligate male cannibalism, in turn, would have dramatically increased the cost of males, and have created a strong selective advantage for cyclic thelytoky and the other features of the *Micromalthus* life cycle that minimize the role of the male.

**Key words:** Coleoptera – Micromalthidae – life cycle – evolution – parthenogenesis – haplodiploidy – paedogenesis – viviparity – thelytoky – arrhenotoky – amphitoky – bacterial endosymbionts – cannibalism – matriphagy

## Introduction

*Micromalthus debilis* LeConte 1878, the sole constituent of the family Micromalthidae (Coleoptera), has been an enigma since its description over a century ago. Of about 17 extant independent haplodiploid clades, only one – *M. debilis* – consists of only a single species (Otto and Jarne 2001) and of seven known independent cyclically parthenogenetic clades, again only one – *M. debilis* – contains only one species (Hebert 1987). It is generally known that various components of this insect's life cycle are unique among Coleoptera and indeed unique among Metazoa. Although most major work on *M. debilis* occurred before 1950, the major features of the beetle's life cycle are well established, although they are not widely known and they are far from being well understood. Here we provide a general introduction to *M. debilis*, review the history of studies of its life cycle, briefly compare it to other species with somewhat similar life cycles, and suggest a novel evolutionary interpretation.

## Taxonomic history

LeConte (1878) described the genus *Micromalthus*, and the species *M. debilis*, based on material collected in rotting wood in Detroit, USA. He placed the genus, with some question, in the family Lymexylidae because of certain morphological similarities between *Micromalthus* and *Hylecoetus* Latreille, 1806, the latter of which is a 'typical' lymexylid. LeConte (1878: p. 613) mentioned that the species is 'feeble and ill-developed', and that *M. debilis* would be expected to have lost the peculiar characters of the maxillary palpi present in all other members of Lymexylidae.

Surprisingly, in the same year and journal volume, Hubbard (1878) provided the first description and figure of the cerambycoid larva of *M. debilis*, as well as the first illustrations of the adult. Hubbard compared the characters of the larvae of *Micromalthus* and *Hylecoetus* and supported LeConte's placement of *Micromalthus* in Lymexylidae based on similarities in

larval antennae and mouthparts. From an historical point of view, it is interesting that the level of analysis presented for the larval stage far surpassed that for the adult.

The first elucidation of the life cycle, although somewhat superficial, was presented in two papers by Barber (1913a,b). These will be discussed more fully in the section on the life cycle of *M. debilis*, but an important taxonomic change occurred in Barber (1913b), who suggested that the family Micromalthidae be erected to accommodate *M. debilis*. However, Barber failed to state where this new family should be placed in the classification of Coleoptera, although presumably he would have placed it near Lymexylidae.

Since then, on the basis of two different character systems, namely the wing-folding pattern of adults and larval mouthparts, Micromalthidae has been placed with Cupedidae in the primitive suborder Archostemata (Forbes 1926; Böving and Craighead 1931). This placement has remained essentially unaltered, reinforced by the fact that Crowson (e.g. 1955, 1975, 1981), Lawrence (1982), Lawrence and Newton (1982, 1995), and Lawrence (1991) supported the archostematan affinities of *Micromalthus*. A detailed study of the larva of *Micromalthus* is given by Beutel and Hörnschemeyer (2002), whose phylogenetic analysis of larval characters places the genus as the sister group of Cupedidae, within Archostemata. Somewhat earlier, however, Arnett (1968) removed Micromalthidae from Archostemata and placed it at the end of Cantharoidea, based on absence of notopleural sutures in the adult. It is tempting to compare the paedogenetic larva of *M. debilis* with a neotenic female adult of Lampyridae (as will be discussed below) and this may have accounted for Arnett placing Micromalthidae immediately after Lampyridae. This new placement, however, was based on little supporting data. More plausibility was added to a non-Archostematan alliance of *M. debilis* by Hennig (1981) who stated that only symplesiomorphies were used by Crowson to group Micromalthidae with the other three families of Archostemata. As is typical with enigmatic taxa, for some authors it was easier to say where Micromalthidae did *not* belong, than it was to say with certainty where

the family did belong. Hennig (1981) stated that *M. debilis* may be a simplified cantharoid or lymexyloid. Despite this, there seems solid consensus that *Micromalthus* belongs in Archostemata, near Cupedidae (authors given above).

## Distribution and diversity

Although it was originally described from, and is apparently native to, the eastern United States (Lawrence 1982), *M. debilis* subsequently has been found in South Africa (Pringle 1938; Paterson 1938), Hong Kong (Marshall and Thornton 1963), Cuba, Brazil and Hawaii (Lawrence 1982), and British Columbia, New Mexico, Florida and Gibraltar (Lawrence 1991). This range expansion apparently represents passive dispersal by humans, as Pringle (1938) stated that *M. debilis* was found in structural timber at a depth of 6000 feet below the surface of the ground in a South African mine. The distribution of *M. debilis* has been examined in detail by Philips (2001), who stated that a recently collected specimen from Belize might represent part of the natural range of the species. Miocene fossil triungulins of *M. debilis* have been reported from Mexico (Rozen 1971). Earlier, the range of the genus *Micromalthus* was wider, as a fossil *Micromalthus* has been reported from Cretaceous Lebanese amber (Crowson 1981).

As an explanation for the presence of *M. debilis* in South Africa, Pringle (1938: 276–77) offered two possibilities. First, the original introduction may have occurred in pine lumber imported from North America. However, as Barber (1913a) mentioned, *M. debilis* inhabits very old wood in the red rot stage of decay. Therefore, since the imported lumber was to be used for constructing underground mine shafts, it is doubtful that badly decayed logs would have been included in the shipment. The other explanation offered by Pringle is that *M. debilis* may also (naturally?) occur in some of the more moist forests of South Africa. It is difficult to speculate on the validity of either hypothesis, although it is generally believed that *M. debilis* expanded its range in historical times through transport of infested lumber and wood products (Lawrence 1982, 1991).

According to the latest classification of Coleoptera by Lawrence and Newton (1995), Micromalthidae is composed of the single species, *M. debilis*. Several papers have appeared concerning the differences between North American, South African and Hong Kong specimens of *M. debilis*. Both Pringle (1938) and Paterson (1938) listed differences between South African and American specimens of *M. debilis*, in the triungulin and cerambycoid larva, and in the adult female. One of the criteria used by Paterson (1938) was the slightly larger size of the South African specimens. Clearly, this difference has little taxonomic or systematic significance; Andersen and Nilssen 1983) suggested that a varied intrapopulation size is common in Coleoptera whose larvae cannot control their nutritional environment. As an example, a tree-boring species of Cerambycidae may exhibit three times the intrapopulation body length variation as in a free-ranging species of Dytiscidae or Carabidae.

Seemingly major differences between Hong Kong and American specimens of *M. debilis* were noted by Marshall and Thornton (1963). For example, they found the triungulin larva to have a single stemma on each side of the head capsule, whereas all previously published descriptions of the triungulin stage from the United States or South Africa did not mention the presence of any stemmata. Despite these differences, some of which are more readily reconciled than others, none of the above authors described a new species of *Micromalthus* based on specimens from South Africa or Hong Kong. However, Lawrence (1991) mentioned that presence of stemmata in the Hong Kong form may be justification for recognition of a species distinct from *M. debilis*.

## Life cycle: an historical review of the evidence

Nothing was stated in the original descriptions of the adult and larvae by LeConte (1878) or Hubbard (1878), respectively, that gave any indication of the bizarre and complex life cycle of this beetle. Had either of these authors known what now is known about *M. debilis*, certainly more importance would have been placed on consideration of its taxonomic and evolutionary significance.

Barber (1913a,b) is credited with first having observed *M. debilis* in detail, and with discovering its basic life cycle. His remarks were based on examination of a field colony and on careful laboratory observations. Barber was given a vial of beetle larvae for identification and noticed three distinct types. One form he recognized as *M. debilis* from the description in Hubbard (1878), but two other distinct forms were present in the sample. These, in fact, were the triungulin and paedogenetic larva of *Micromalthus*. Barber (1913a: p. 33) thought the robust larva from one of his colonies to have been a prepupa, but 'this hypothesis was shattered…when embryos began issuing alive, but in an oval shape, from the ventral surface, close to the tip of the body of one that had shortly before been isolated in a small vial'. Barber had discovered the paedogenetic component of the life cycle, as well as the triungulin (caraboid, or legged larva), cerambycoid and reproductive larvae. As a summary of the life cycle, Barber (1913a: p. 35) listed five distinct forms: (1) viviparous larviform, reproductive stage, giving birth to (2) legged larvae which molt into (3) legless larvae, giving rise to either (4) pupae or (5) winged adults. Barber compared the situation discovered in *M. debilis* to the extreme sexual dimorphism exhibited in the beetle family Phengodidae. However, at that time, the fact that *M. debilis* reproduced parthenogenetically was unknown, and Barber speculated how the paedogenetic larvae could be fertilized while deep inside wood, or underground.

Significant additions to knowledge of the life history of *M. debilis* were made in a second paper by Barber (1913b). The timing of the various larval instars was noted, based on extended laboratory observations. The caraboid or triungulin larva feeds for about a week, after which it moults to the cerambycoid larva. This form may moult once or twice additionally without significantly changing form. It then bores through the wood for several months, during which the ovaries of the next instar become apparent. After becoming quiescent, the cerambycoid larva moults to the paedogenetic larva, or, very rarely, to a pupa. The young larvae are born in two weeks and average 10 in number.

For the first time, the sex-determination mechanism, or at least the sex segregation mechanism, was described by Barber (1913b). Some paedogenetic larvae die apparently without giving birth, and others produce a single, large egg which remains attached to the outside of the mother larva. In about 10 days, this egg hatches to a form unlike any other; it was called the curculionoid larva. This larva inserts its head into the exit system of its mother and devours her body contents.

Once fed, it moults into what Barber called the metrophagous larva, after which pupation occurs. Only adult, winged males are produced in the above manner. Barber (1913b) felt that this radically divergent life cycle was a hindrance to inbreeding because it was much easier to produce a winged female than a winged male. Therefore, by the time the latter is achieved, the females would be either dead, or otherwise unavailable for mating with their male siblings.

To more fully explore the hypermetamorphosis of *M. debilis* larvae, Barber (1913b) isolated 21 caraboid larvae and 2 months later, the contents of the vials were examined. Of 16 survivors, the following number of different forms were found: seven cerambycoid larvae, two of which were very close to moulting to the paedogenetic larva; four paedogenetic larvae without apparent embryos; two were eaten after having given birth to larvae; two paedogenetic larvae with a male egg on each; and one pupa of the adult female. It is important to note here, as Barber did, that since the wood for all these larvae was at a similar stage of decay and was kept under the same conditions, the variety of forms arising from the caraboid larvae could not simply be attributed to action of environmental factors present in the rearing medium. In his two papers, Barber made significant initial advances in knowledge of *M. debilis*. The only life stages he did not observe were eggs and larvae produced from an actual mating between normal males and females. The diagram which Barber (1913b) used to illustrate the life cycle of *M. debilis* is reproduced (after Pringle 1938) in Fig. 1.

Surely these two early papers, with their descriptions of the very strange life cycle of *M. debilis*, must have been met with some skepticism. Although Barber was correct on almost every point, Scott (1938) attributed the distrust of Barber's findings to the latter's lack of illustrative evidence. One critic who actually published his disagreement was Caillol (1914), who never once actually studied *M. debilis* himself. Caillol's major points of contention were as follows (from Pringle 1938): (1) the caraboid larva of Barber should properly be called a triungulin, as the hypermetamorphosis of *M. debilis* is basically similar in design to that of Meloidae; (2) the paedogenetic larva is actually a degenerate, wingless, parthenogenetic adult female. Pringle (1938) presented a diagrammatic representation of Caillol's alternative hypotheses; this is given in Fig. 2.

Pringle (1938) agreed that the first instar larva of *M. debilis* was not truly caraboid, because it lacked the prominent urogomphi and typical carabid-like antennae. He agreed that 'triungulin' was a more appropriate name for this larval stage. However, on the second point of contention, Pringle did not agree with Caillol, and gave three arguments against calling the paedogenetic larva a neotenic female (Pringle 1938: p. 274). Since, in *M. debilis*, the larvae of the next generation are already partially developed in the cerambycoid larva, the form which succeeds it must be a paedogenetic larva. Also, the mouthparts of the paedogenetic larva, although reduced, resemble closely those of the cerambycoid larva. Finally, there is no evidence of a pupal, or other resting stage between the cerambycoid and paedogenetic larva. In other groups of
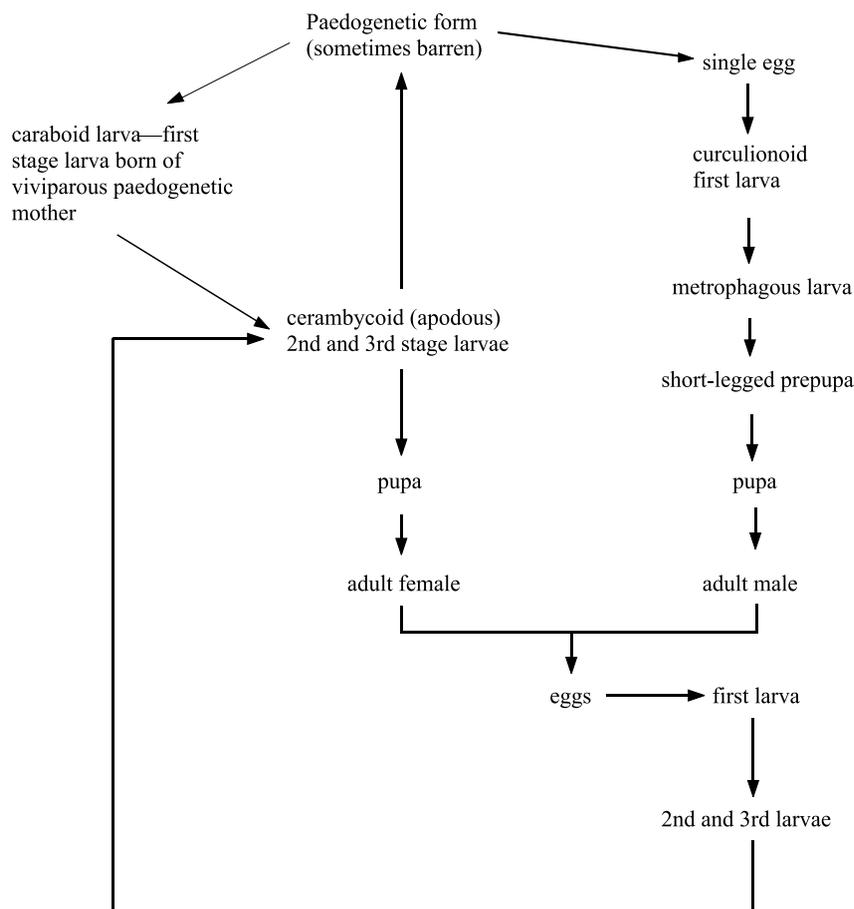


Fig. 1. Diagrammatic representation of the life cycle of *Micromalthus debilis* LeConte according to Barber (1913b) (after Pringle 1938)
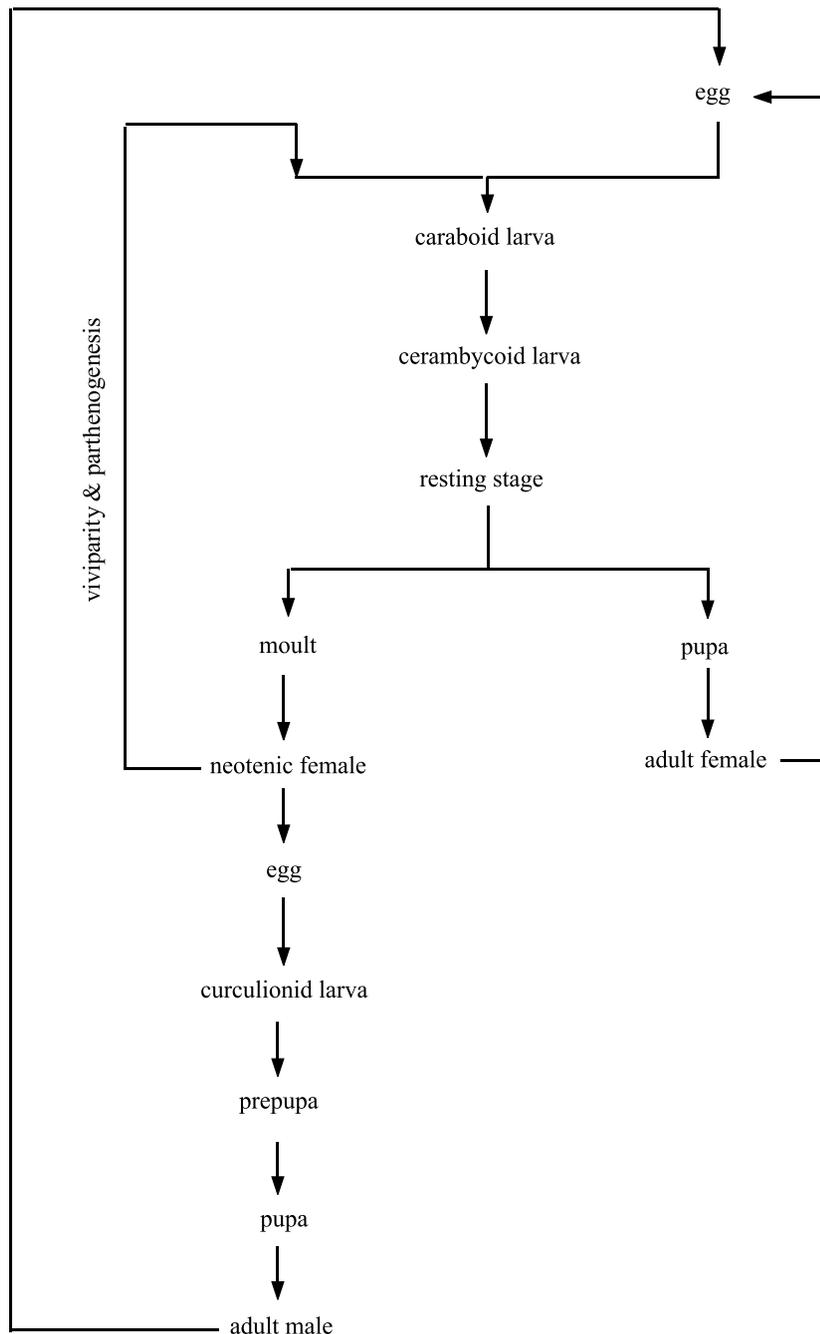
Fig. 2. Diagrammatic representation of the life cycle of *Micromalthus debilis* LeConte according to Caillol (1914) (after Pringle 1938)

Coleoptera exhibiting neoteny or paedomorphosis such as Phengodidae and Lampyridae, a female pupal stage is present (Crowson 1981). Therefore, we agree with Pringle's assessment that the larviform reproductive stage of *M. debilis* is in fact a larva, and not a neotenic female in the sense of the same stage in several families of Cantharoidea. Although Pringle's (1938) paper added nothing new concerning the life cycle of *M. debilis*, relatively detailed descriptions and illustrations were given of the three 'female' larvae and the pupa of *M. debilis*.

Perhaps the most important and illuminating examinations of *Micromalthus* were published by A. C. Scott in a series of papers from 1936 to 1941. No previous worker had actually examined the cytogenetics, spermatogenesis, or structure of the gonads of *M. debilis* when in fact, its life cycle is at least in part, merely a manifestation of these internal features.

Scott (1936) discovered, and first documented, that males are haploid in their germ line cells throughout development whereas females remain diploid. From examination of cleavage nuclei in developing eggs, Scott found the diploid number of chromosomes to be 20. However, since the counts were taken early in cleavage, the possibility of chromosome elimination was not discounted. A detailed study of spermatogenesis revealed unipolar spindle fibres, and an abortive first division resulting in only two spermatozoa being produced from each primary spermatocyte. Based on these findings,

Scott (1936) challenged several previously accepted theories about meiosis and spindle fibre formation.

The life cycle of *M. debilis* was most clearly documented by Scott (1938), who considered internal reproductive structures worthy of study. Five reproductive forms were named by Scott (1938: 635): (1) thelytokous (female-producing) paedogenetic larva; (2) arrhenotokous (male-producing) paedogenetic larva; (3) amphit[erot]okous (female- and/or male-producing) pae-dogenetic larva; (4) adult female; and (5) adult male. The three types of paedogenetic larvae are impossible to distinguish until the middle of the penultimate instar. At this time, the thelytokous larva can be identified by the presence of elongating eggs and young embryos. The male-producing larva is distinguished by its opaque white colour, and its more cylindrical shape with distinct abdominal segmentation.

Barber (1913b) thought that the paedogenetic larva was occasionally barren, i.e. had not given birth to any larvae. Scott (1938) discovered an amphitokous form; these larvae were dissected and found to be basically arrhenotokous, but not to have successfully shed their male eggs. When this male egg is aborted or otherwise fails to develop, thelytokous eggs are subsequently produced by such larvae. This may explain why Barber (1913b) found four larvae without apparent embryos, in his isolation experiment described above. Scott (1938) mentioned that the ovaries of each type of paedogenetic larva are distinctive, but that the characteristics of each are attained only gradually. From the small, undifferentiated ovary of first stage female larvae, three outcomes are possible (Scott 1938: p. 642): (1) the small, possibly abortive, ovary of the adult female with only one or several eggs; (2) the ovary of the arrhenotokous larva with relatively larger eggs and robust pedicels; or (3) the large ovary of the thelytokous larva with cylindrical eggs. Each follicle of type 3 serves as a brood chamber for a single embryo. In all paedogenetic larvae, there is no uterus, vagina, or spermatheca (Scott 1938). The adult female, however, has a more typical reproductive system with these three structures present.

The amphitokous larva held much interest for Scott and in 1941, he published a treatment of the various components of production of males in *M. debilis*, including the reversal from male to female production. Various questions were posed: (1) why is only one male produced from the arrhenotokous larva when its ovaries may contain several eggs? Scott (1938) indicated that of approximately 200 arrhenotokous larvae examined, 1% had one egg in both ovaries, 71% had two, 23% had three and only 4% had four eggs; (2) does the relative age and/or position of the male egg within the ovariole influence its chances of being used?; and (3) if the larva of the shed egg is prevented from eventually consuming its mother, can the arrhenotokous larva release another male egg?

Scott (1941) could not answer the first question, and found no evidence to support his hypothesis that either age or position had an influence on an embryo's chances of being shed. It was thought that since a male larva's sole source of food is the paedogenetic mother, multiple births would cause competition for this resource. Scott (1941) envisioned a 'physiological cooperation' between the shed male embryo and its mother. A possible mechanism was suggested to be a hormone, the release of which may be triggered by exit of the egg. This hormone would then cause the muscular contrac-tions, which normally expel the eggs, to cease.

If the male embryo is removed from the female or does not complete development, a new brood of female larvae is formed, after about 4 weeks. The development and birthing processes of these reversed female larvae are exactly the same as those of larvae produced for ordinarily thelytokous paedo-genetic larvae. The brood size of this reversed arrhenotokous larva is intermediate between that of a normal thelytokous and a normal arrhenotokous paedogenetic larva. Scott (1941) found that occasionally, amphitokous larvae produced new female larvae even though male embryos had not been shed. Therefore, the mechanical removal of the male embryo is not the reason for development of the new batch of female larvae. The oogonia which eventually contribute to development of female embryos are present in the amphitokous larvae before the male embryo is shed. These proliferate in undeveloped ovarioles which do not fully form during growth of the male eggs.

## Life cycle: evolutionary perspectives

One might suppose that because of the extremely aberrant life cycle of *M. debilis*, this species would be the focus of much research on functional and evolutionary biology. Unfortu-nately, this has not occurred. There have been no significant accounts of any aspect of the natural history of *M. debilis* since the work of Scott (1936, 1938, 1941). Many critical aspects of the reproductive biology of *M. debilis* remain to be investi-gated in detail, for example, oogenesis (Smith 1971). It is not even known whether their parthenogenesis is apomictic or automictic. There have, however, been significant advances in recent decades in the study of partially analogous life cycles in other taxa, and in the theoretical issues involved. Here we seek to place *M. debilis* in a broader context of empirical and theoretical studies of metazoan life cycle diversity.

### Cycles of arrhenotoky and thelytoky

Cyclic parthenogenesis (cyclic thelytoky) is one of the most infrequently arising genetic systems in animals, having origin-ated as few as seven times. One requirement of the genetic systems of cyclic parthenogens is that there can be no elements of strictly paternal inheritance such as Y chromosomes (Hebert 1987). Indeed, most cyclic parthenogenetic clades (four of seven) are like *Micromalthus* in having effectively haplodiploid inheritance, either through paternal genome elimination in males (in *Heteropeza* and related cecidomyiid midges) or through arrhenotoky (in *Micromalthus*, in the wasp family Cynipidae and in the rotifer class Monogononta). In Cecidomyiidae and Cynipidae, it is clear that the origin of effective haplodiploidy preceded the origin of a thelytokous phase of the life cycle (Hebert 1987), but in *Micromalthus* (as in Monogononta) we do not know which came first, because haplodiploidy and cyclic parthenogenesis originate along the same long phylogenetic branch.

It has been reported that *Micromalthus* males are sexually non-functional (Smith 1971; White 1973), which would make *Micromalthus* an effectively completely thelytokous lineage and indeed a champion 'ancient asexual' (Judson and Normark 1996). However, given absence of any other exam-ples of comparably ancient insect lineages that are completely thelytokous, given the frequency with which functional males are discovered where previously thought to be absent (e.g. Blackman et al. 2001), and given the evolutionary importance of even small amounts of genetic exchange, it is unwise to dismiss *M. debilis* males as completely non-functional.

## Paedogenesis

The apparently odd complexity of the *Micromalthus* life cycle is best understood in the context of other cyclically parthenogenetic groups, among which it does not seem so unusual. It is a general feature of cyclic parthenogens that there are two physiologically different types of propagules, one of which is produced sexually whereas the other is produced asexually. The existence of two propagule types is probably required both for the origin (Hebert 1987) and the evolutionary stability (Burt 2000) of cyclic parthenogenesis. In a bare majority of cases (four of the seven cyclically parthenogenetic clades), the two propagule types are egg versus larva. Indeed, these four viviparous, cyclically parthenogenetic clades illustrate that two propagule types is a minimum: all of them have more complex cycles of successive viviparous morphs. In aphids (whose 'larvae' are fairly adult-like nymphs) the first viviparous morph (the 'fundatrix') is usually very different from subsequent morphs. In digenean trematodes, the asexual generations proceed from sporocyst to redia to cercaria. As reviewed above, the viviparous generations of *Micromalthus* proceed from triungulin larva to cerambycoid larva. *Heteropeza* and related cecidomyiids also have a complex cycle: Scott (1938) was sufficiently impressed with the parallels between *M. debilis* and *Heteropeza pygmaea* Winnertz, 1846 (which he called *Oligarces paradoxus* Meinert, 1865) that he listed 10 shared developmental stages. When chromosomal changes are taken into account, the cycle of *H. pygmaea* is seen as even more complex (White 1973).

Reproduction by larviform individuals is frequently seen in other effectively haplodiploid groups that inhabit dead wood, even those that are not cyclically parthenogenetic, although in these often it is the male that is larviform. Cecidomyiidae is one of two dipteran families that display paternal genome elimination. The other is Sciaridae, which includes *Plastosciara,* in which both sexes are neotenic (Hamilton 1978) and *Micromalthus* is one of two beetle clades that are arrhenotokous: the other arrhenotokous beetle clade occurs in the Curculionidae (subfamily Scolytinae), and the most basal lineage of that clade is the genus *Ozopemon* (Jordal et al. 2000), which has neotenic males.

Another example of an association between the origins of an essentially haplodiploid system and paedogenetic females is arguably seen in the scale insects (superfamily Coccoidea), in which the origin of the paternal genome elimination system in males coincides approximately with the origin of the Neococcoidea, which have a notably larviform female morphology (Gullan and Kosztarab 1997; Herrick and Seger 1999).

## Obligate matriphagy by males

Another clue that males may be functional is the very high cost of producing one, since males obligately eat their mothers. This would presumably create strong selection for elimination of males if they were purely vestigial. Matriphagy occurs in other insects (Kohno 1997) and arachnids (Toyama 1999; Kim et al. 2000) but *Micromalthus* may be unique in having obligate matriphagy that is specific to males, and is certainly unique among cyclic parthenogens in having matriphagy. *Micromalthus* has so many unique features that it is very difficult to know which came first, but one plausible candidate for a key evolutionary innovation in *Micromalthus* is obligate cannibalism by males. This may have precipitated a crisis in micromalthid evolution that drove the minimization of the role of the male in the life cycle.

Why are larval *Micromalthus* males obligately cannibalistic? Larval female *Micromalthus* feed on rotting wood, which can be a nutritionally poor resource. Many insects using it are dependent for some nutrients on endosymbiotic bacteria or fungi (Buchner 1965). Gram-positive bacteria are present in the ovarioles and haemolymph of *Micromalthus* as well, although their role has not been investigated (Kühne 1972). Hamilton (1993) pointed out that from the perspective of a transovarially transmitted endosymbiont, a male is a dead end, and raised the question of why endosymbionts in males are functional rather than senescent or absent. *Micromalthus* may present a case in which maternally inherited endosymbionts are indeed non-functional in males. Hamilton (1993) speculated that endosymbionts function in males in order to benefit related endosymbionts in the males' mates. The non-synchronous production of reproductive males and females of *Micromalthus* restricts opportunities for inbreeding (compared to the inbreeding haplodiploid species Hamilton was considering), which may lead to reduced selection on endosymbionts to promote male function. Males with senescent or otherwise non-functional symbionts may be forced to seek out more nutritious food sources whose digestion does not require participation by the endosymbionts – often, the only such food sources available in *Micromalthus'* habitat would be conspecifics. Documented cases of absence or degeneration of endosymbiotic bacteria in males may be found in the scale insects (Tremblay 1977) – another group with paedomorphic females and functional haplodiploidy. Cannibalism by male offspring but not female offspring would essentially hijack the mother's sex-allocation decisions and result in highly male-biased secondary sex ratios within broods. This would simultaneously increase both (1) the cost of producing males, and (2) the population-wide ratio of adult males to adult females. Both of these effects would exert strong selection on females to produce female-biased primary brood sex ratios (Charnov 1982). The high cost of males in particular would favour thelytoky. The life cycle of *Micromalthus* could thus be interpreted as a consequence, in large part, of obligate cannibalism by males.

It may be objected that there are many outbreeding groups dependent on maternally inherited endosymbionts for nutrition – for instance, aphids – in which males feed and are functional (Buchner 1965). This is empirically true, but as Hamilton (1993) pointed out, it is theoretically paradoxical that the endosymbionts should be acting for the benefit of unrelated organisms. One must hypothesize, ad hoc, that the endosymbionts in outbreeding male aphids lack the capacity for sex discrimination, or that they are successfully manipulated by their hosts, or that their activity is favoured by higher-level selection (i.e. endosymbionts that acquire the ability to discriminate against males may drive their host species to extinction). Depending on these factors, a range of possible relationships between endosymbionts and males may be expected. The scenario presented here for *Micromalthus* – non-functionality of endosymbionts in males – is perhaps the simplest such relationship to account for in terms of theory.

Matriphagy in *Micromalthus*, as in other cases, seems to be predicated on the 'consent' of the mother, in view of her torpor following the production of a male offspring. Why does the mother submit to matriphagy? Note that (1) males are apparently produced in response to stress (drying out of the habitat), and (2) male offspring have no fathers, all their genes being maternal. Haplodiploidy has been compared to hermaphrod-

itism, in that a single female produces both eggs and 'gameto-biont' males, genetically equivalent to sperm. Most haplodiploid organisms are analogous to simultaneous hermaphrodites, in that a female can facultatively switch between producing males and producing females. But *Micromalthus* is more closely analogous to a protogynous sequential hermaphrodite, in that a reproductive female individual can 'transform herself' (by producing a single male larva that consumes her) into a male, albeit while simultaneously discarding half her genome. She apparently takes this step only in event of environmental crisis, when nothing is to be gained from further attempts at reproduction or even persistence within the same habitat.

Alternatively, we might understand cannibalism by male *Micromalthus* in terms of the pugnacious nature of many male insects (Hamilton 1979), especially when males are wingless and rare compared to females, and especially in enclosed habitats such as rotting logs (Hamilton 1978, 1979). Although intuitively, we might expect male competition and violence mostly between non-relatives, in fact it can be intense even between very close relatives (West et al. 2001). Conceivably, matriphagy by a male could be selectively favoured if the mother might otherwise bear brothers who would be non-genetically identical ($r = 0.5$) reproductive competitors. Difficulties for this hypothesis include (1) the wings of male *M. debilis*, suggesting dispersal and unlikely competition with brothers, and (2) the mother's collusion in the matriphagy. Nonetheless, it is not known whether any predispersal mating occurs, and it remains possible that pre-emptive fratricide is an additional benefit of matriphagy for male *Micromalthus*.

## Concluding remarks

*Micromalthus* is an excellent example of a number of intriguing apparent correlations across the life cycles of insects and other animals. Various authors have remarked on various correlations between the following characteristics: the dead-tree habitat, dependence on endosymbiotic bacteria, polyphagy, haplodiploidy, cyclical parthenogenesis, highly polymorphic life cycle, paedomorphosis, and female winglessness (e.g. Hamilton 1978, 1993; Hebert 1987). Although *M. debilis* is only one species, taxonomically isolated, and although we may never know the phylogenetic order in which its many novel life-cycle characters were acquired, it takes its place alongside much larger clades as a crucial example of genetic-system innovation. It is by comparing these several clades – however, large or small each may be – that we will gain insight into the causes of genetic system evolution. Because *M. debilis* is not so different ecologically from Cupedidae, we have a relatively clear understanding of the ecological context in which haplodiploidy arose in Micromalthidae. This is more than we can say for Hymenoptera, where diversification (both of the order and of its sister group the Mecopterida) has obscured the context of haplodiploidy's origin. Although we can learn endless lessons about the consequences of haplodiploidy from studying Hymenoptera, ultimately we will learn more about its origins from further study of *Micromalthus*.

## Acknowledgements

## Zusammenfassung

*Der Lebenszyklus von Micromalthus debilis LeConte 1878 (Coleoptera: Archostemata: Micromalthidae): historischer Überblick und evolutive Perspektive*

Der Lebenszyklus von *Micromalthus debilis* LeConte 1878 ist der bizarrste innerhalb der gesamten Metazoen. Die Reproduktion ist im typischen Fall durch Thelytokie, Viviparie und larviforme Weibchen charakterisiert, aber auch eine arrhenotoke Phase kommt in seltenen Fällen vor. Das aktive erste Larvenstadium (Triungulinus) entwickelt sich zu einer beinlosen Larve die Nahrung aufnimmt (cerambycoide Larve). Diese verpuppt sich, was zum späteren Schlüpfen eines diploiden, adulten Weibchens führt, oder entwickelt sich zu einer von drei folgenden reproduktiven pädogenetischen Formen: (1) ein thelytokes Weibchen, das lebendgebärend Triungulinus-Larven hervorbringt; (2) ein arrhenotokes Weibchen das ein einziges Ei produziert, das sich zu einer kurzbeinigen Larve entwickelt (curculionoide Larve), die ihrerseits das Erzeugertier verzehrt und sich zu einem haploiden adulten Männchen entwickelt; oder (3) ein amphitokes Weibchen, das beide reproduktiven Wege beschreiten kann. Wir vermuten, daß *Micromalthus* von mütterlicherseits übertragenen Bakterien abhängt, um verrottendes Holz verdauen zu können, und daß diese Bakterien in Männchen degeneriert sind. Dadurch wird im männlichen Geschlecht Kannibalismus obligatorisch. Obligatorischer Kannibalismus bei den Männchen würde wiederum die Kosten der Produktion von Männchen drastisch erhöhen. Daraus ergibt sich ein starker selektiver Vorteil für die zyklische Thelytokie und für andere Besonderheiten des Lebenszyklus von *Micromalthus*, die die Rolle des Männchens minimieren.

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