LIFE HISTORY AND BIOLOGY OF CALOGLYPHUS ANOMALUS NESBITT (ACARINA : ACARIDAE) [1]

BY

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A study of the recently described species *Caloglyphus anomalus* Nesbitt 1944 was initiated here to gain information on the biology of this poorly known genus on which little work had been done since that of SCHULZE (1924). This mite was first recorded from Colorado in 1963 (PILLAI and WINSTON, 1963), and the adult forms were described in detail at that time. The present paper describes the developmental stages, including the hypopus which was first reported by PILLAI and WINSTON (1968). This species is of special interest as favorable material for the study of the inducement and formation of hypopi and of two different, functioning types of males. Further, it can be separated, with *C. paranomalus*, from the rest of the genus by the absence of anal suckers in the male. NESBITT (1949) suggested that they were derived from a common ancestor which underwent mutation rather recently.

MATERIALS AND METHODS.

The technique used for mass rearing and individual culturing of these mites has already been described (PILLAI and WINSTON, 1968). *Escherichia coli* on Bonner's medium served as the food source throughout this work. Life history studies were carried out in microcells starting with one egg in each cell. The egg was surface-sterilized with 2.0 % " Chlorox " solution or with 0.2 % sodium hypochlorite (erroneously reported as 2.0 % in PILLAI and WINSTON (1968)) for 20 minutes before it was placed on the substrate. In some of the oviposition studies, porcelain filter rings inserted on the media served as enclosures. All cultures were maintained at 100 % R. H. because of the sensitivity of the mites to desiccation.

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Temperatures of 15, 20, 25, 30 and 35° C. were used. Observations were made every 12 hours under a stereo microscope. Morphological studies of the various stages were made using either temporary lactic acid mounts or permanent preparations in Hoyer's medium; mites were always first cleared in Nesbitt's solution. Morphological terminology follows that of GRANDJEAN (1939) and HUGHES (1961).

LIFE HISTORY.

Egg (Fig. 1).

Eggs are oval, about 137 μ long and 85 μ broad, cream colored and with a smooth chorion. They are laid singly or, occasionally, in batches. The largest percentage of hatching was observed at 20° and 25° C. with 100 % R.H. (Table 1). The time taken for hatching also varied with temperature: 6.8 days at 15° C., about 4 days at 20° C and 25° C. and 2.4 days at 30° C. Eggs raised at 35° C. failed to hatch. During eclosion the pulsating movement of the emerging larva helped by the pressure of the gnathosoma, the bruststieles, and the unfolding legs, break the egg shell at the opisthosomal region and cleave it laterad (Fig. 2). The larva pulls itself out and the chorion is cast aside as an open, bivalved box. The bruststieles are turgid and held erect for a short time after emergence.

TABLE 1.

Life history studies.

			Average number of days spent in various stages.								
Series No.	Temp. °C.	% Eggs hatched	Egg	Larva	Larval quiescence	Proto-nymph	Proto-nymphal quiescence	Trito-nymph	Trito-nymphal quies-cence	Preovi-position period	Total n°. of days from egg to adult
1.	15	52.0	6.75	2.5	0.63	2.0	0.75	1.25	0.88	3.88	14.8
2.	20	72.2	3.75	1.38	0.62	1.25	1.13	1.25	0.62	2.13	10.00
3.	25	78.2	3.88	0.88	0.62	1.38	0.5	1.38	0.62	no data	9.3
4.	30	50.0	2.4	0.75	0.5	0.5	0.5	0.62	0.75	1.25	6.00

Larva (Figs. 3 and 5).

Length of idiosoma 180-316 μ

Propodosomal shield not clearly formed; supracoxal seta absent; sc i, d_1 and d_2 extremely small; d_3 and d_4 bristle-like, subequal, but less than half of sc e; h e and l p equal; post-anal seta as long as d_4, arising on a line with the posterior extremity of the anus; bruststieles long and expanded at the tip, genital opening and genital suckers absent. ω_1 of tarsi with short, stalk-like region and a prominent distal expansion ; a a, ω_2 and ω_3 absent ; expansions of falcate setae very feeble.

The newly emerged larva walks about randomly at first, but as it nears a bacterial mass it exhibits an increasingly directional movement toward its food. The larva feeds voraciously and more or less continuously for approximately 1 day. A short period before the end of this active stage, it ceases feeding and seeks a drier environment.

The larva then becomes distended with gnathosoma bent downward, and the quiescent stage is formed (Fig. 4). This can be seen either free or glued to a surface. Before entering into the resting stage, the entire body is coated by a sticky substance which dries leaving a glistening appearance. Sometimes particles of sand and such adhere to this coating. If a dry, favorable environment is not available, the larva will go into quiescence even on the wet bacterial streaks in culture cells. After 12 to 18 hours it moults into a protonymph, and the exuvium is cast aside.

Protonymph (Fig. 8).

Length of idiosoma 338-480 μ.

Propodosomal shield clearly visible ; supracoxal seta extremely small, visible only under phase contrast in well cleared preparations ; sc e more than ten times as long as sc i ; d_1 slightly smaller than d_2, d_3 6-8 times as large as d_2, d_4 almost equal or slightly longer than d_3, d_3 and d_4 more hair-like compared to the bristle-like setae of the larvae, d_3 extending slightly beyond d_4 ; genital slit between coxae IV flanked by a pair of genital " suckers " and genital setae ; sa e and sa i present, the latter about ten times as long as the former ; three pairs of anal setae flanking the anus ; a pair of post anals present ; aa and ω_2 present on tarsus I ; setae absent on femur and tibia of leg IV.

The feeding behavior of the protonymph is very much like that of the larva. At 20° C. and 100 % R.H. the protonymphal stage lasts for 1.25 days on the average. A few hours before termination of this stage it assumes the non-feeding phase and responds positively to a drier environment. The quiescent stage succeeding the protonymph lasts for 1.1 days at 20° C. at the end of which it moults and becomes either a deutonymphal hypopus or a tritonymph.

Hypopus (Figs. 6, 7 and 9).

Length of idiosoma = 230-294 μ.

Body creamy white with broadly pointed rostral region and rounded posterior end ; edges of gnathosoma convex, aristae longer than gnathosoma ; propodosoma triangular about one-fourth of hysterosoma ; sc setae subequal ; five pairs of medial dorsal setae on the hysterosoma, first and third displaced lateral to the others.

Sternal shield demarcated laterally by epimerites II ; coxal shield III prominent, but that of IV fused with the genital ; suckers present on coxal shields I and III and on genital shield, a pair of setae close to the latter ; sucker plate slightly longer transversely than broad with a pair of large central disc-shaped suckers having minute radiating marginal strands on the rim visible under phase contrast, another equally large pair of plane discshaped areas on the antero lateral region, and three pairs of marginal suckers of which the two posterior pairs are cup-shaped.

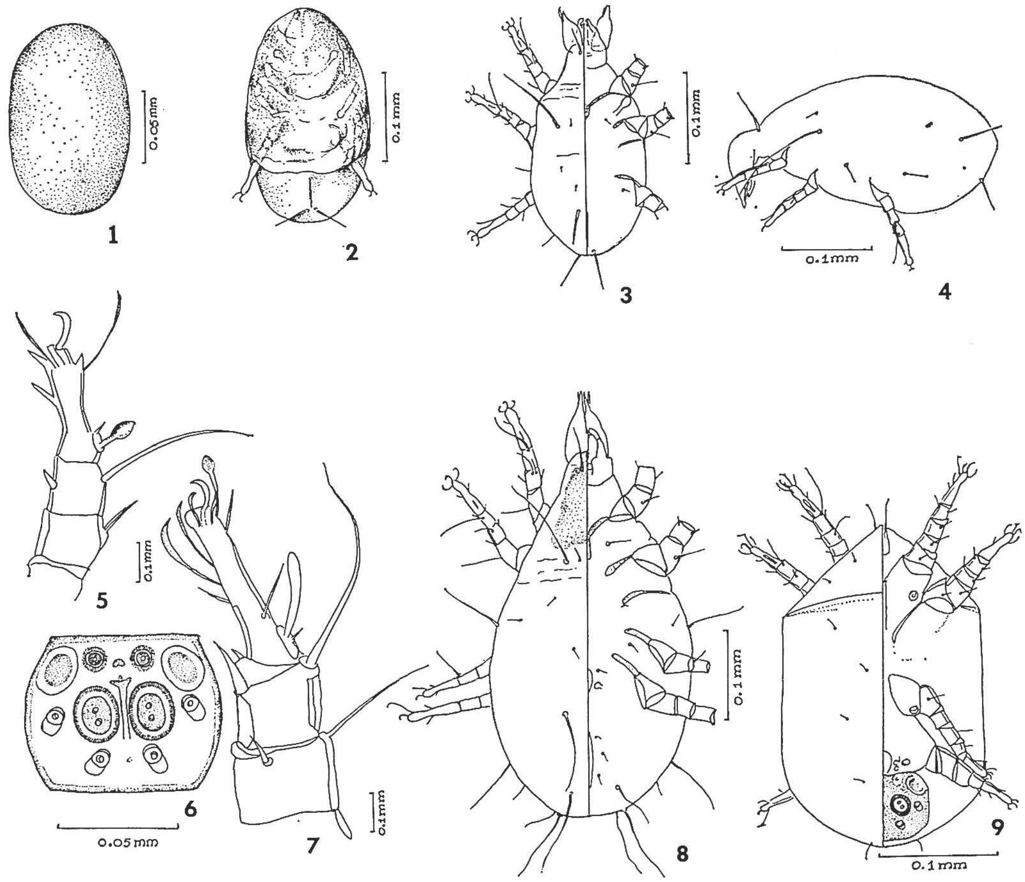


FIG. 1-9 : *Caloghyphus anomalus* Nesbitt.

1. — Egg. 2. — Larva emerging from the egg. 3. — Larva. 4. — Quiescent stage of larva. 5. — Dorso-lateral view of genu, tibia and tarsus of leg I in larva. 6. — Sucker plate of hypopus. 7. — Dorso-lateral view of genu, tibia and tarsus of leg I in hypopus. 8. — Protonymph. 9. — Hypopus.

Tarsus I with four falcate setae ; e saucer-shaped ; ω_1 about 1/2 the length of tarsus, a small spine closely associated with ω_1 at its base ; ba long, more than three-fourths of ω_1, hT a prominent spine in tibia I and II ; σ seta on genu I long, more than half of tibial seta ; leg III very small, not seen when the animal moves ; claws long and sickle-shaped in all the legs ; pulvilli very poorly developed.

The formation of hypopi was frequently associated with declining cultures, but the precise triggering mechanism is not known. This stage can be terminated however by supplying them with fresh food. Hypopi introduced on fresh medium were observed to go into quiescence within a day. Moulting to the tritonymph soon occured and normal development to the adult followed. Females and both heteromorphic and homeomorphic males were represented in populations raised from hypopi.

The suckers and the long hook-like claws of the hypopi are efficient devices for clinging to other animals for transport and distribution. By itself the hypopus can move faster than the other stages and thus spread over short ranges, but making use of other animals for transport seems to be the method for moving long distances. The hypopi frequently raise the anterior part of the body and extend the first pair of legs when moving on the flat culture medium especially when a large object approaches them. This behavior appeared to be an active searching for contact with hosts to which they could cling.

Tritonymph (Fig. 10).

Length of idiosoma 458-654 μ.

sc e about nine times as long as sc i ; d_1 about half of d_2 ; d_2, d_3 and d_4 almost of the same proportions as in protonymph ; a pair of small additional setae present almost on line with the extremity of apodeme IV ; genital slit flanked by two pairs of genital " suckers " and two pairs of setae ; post anals situated farther behind anus than in protonymph ; tarsus I provided with the full adult complement of setae ; setae present on femur and tibia IV.

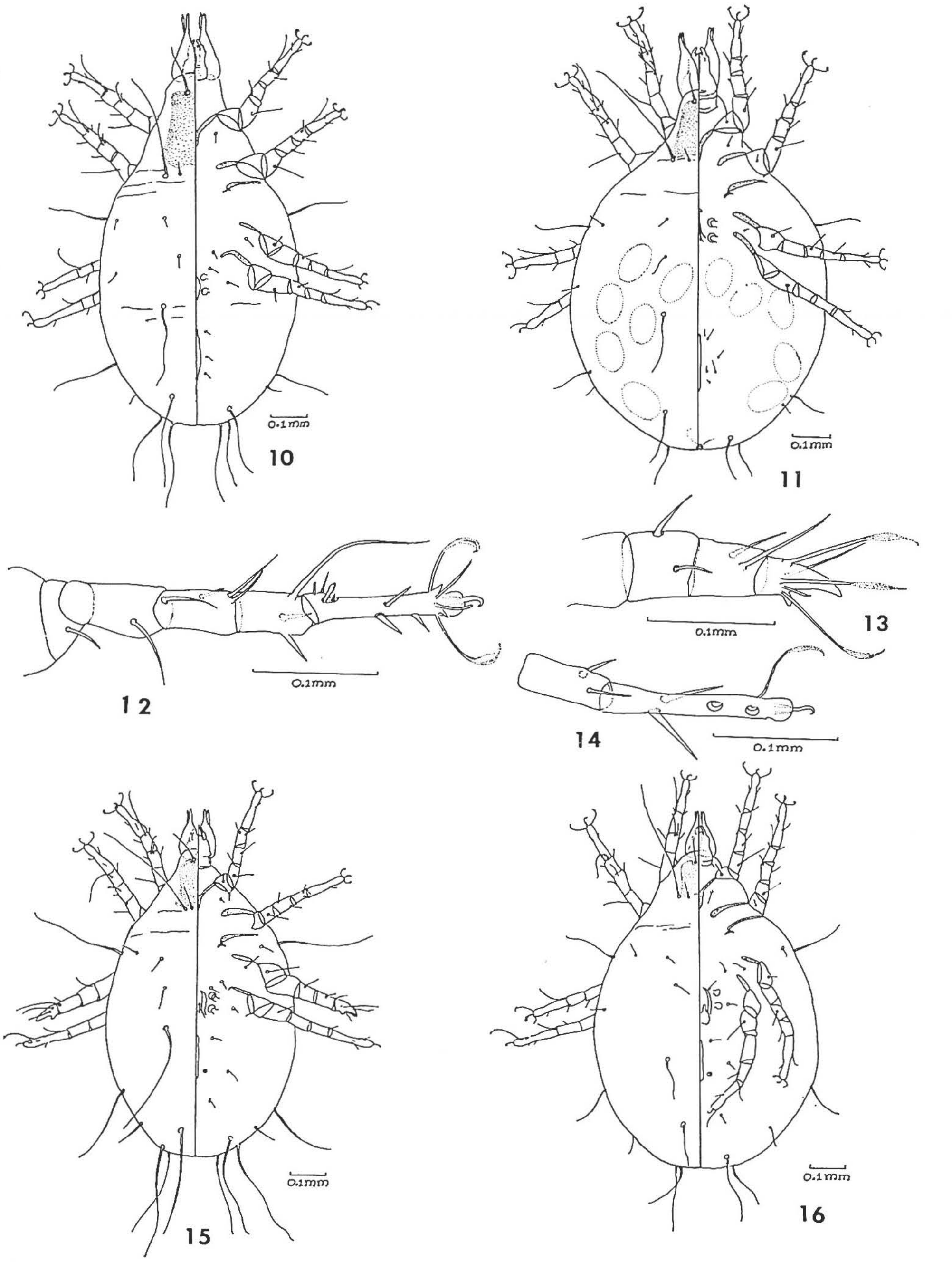
In appearance this stage very much resembles the protonymph and size is not always a clue to diagnosis since it fluctuates depending on the nutritional conditions on the substrate. However, the two pairs of genital " suckers " and the additional pairs of setae, one flanking the genital slit and the other near the extremity of apodeme IV, are reliable guides to identification.

Adult (Figs. 11, 12, 13, 14, 15 and 16).

For complete descriptions of adult forms, see Pillai and Winston (1963).

C. anomalus produces both homeomorphic and heteromorphic males. The striking feature of the latter is the hypertrophied leg III, but the relative length of the setae and the narrowed opisthosomal region help to identify them in large populations. The homeomorphic males have a comparatively rounded body and are slow moving. Both the males lack anal suckers but are provided with suckers at the distal part of tarsus IV.

The females are sluggish, particularly when they are advanced in age. In all our cultures there was a preponderance of females over males.



FIGS. 10-16 : *Caloglyphus anomalus* Nesbitt.

10. — Deutonymph. 11. — Female. 12. — Dorso-lateral view of leg I in male. 13. — Dorso lateral view of genu, tibia and tarsus of leg III in heteromorphic male. 14. — Dorsal view of tarsus IV in males showing tarsal suckers. 15. — Heteromorphic male. 16. — Homeomorphic male.

Biology and Behavior.

Longevity.

At 20° C. mated males lived for 45-59 days whereas mated females under identical conditions had a shorter life span of 31-45 days. This may be due to the fact that in mated females eggs accumulate inside the body making it difficult for her to carry them. If the mite falls on its side it cannot recover because of its size and short legs.

The maximum longevity observed was 112 days in an unmated male and female at 15° C. It is not known how much longer the mites would have lived if they had not died from fungal overgrowth of the culture.

Feeding.

The chelicerae are provided with teeth both on the movable and fixed digits although the mites preferentially feed on materials of a semifluid consistency. While feeding, the gnathosoma is held at right angles to the body. The chelicerae are constantly in motion back and forth and in this way they draw food into the mouth.

Although cannibalism was not noticed as a general behavior, the dying and immobilized mites were occasionally preyed upon by active ones. When the body was punctured mites gathered to feed on the exuded hemocelic content.

Copulation.

Mating takes place a day after the adults have emerged. The hypertrophied third legs of the heteromorphic males help in mounting, but both the males use the fourth pair of legs to hold fast in the oriented position. As in other acarids the sexes orient in opposite direction and the penis is introduced into the bursa of the female situated in the opisthosomal extremity. Copulation lasts from about three minutes to more than half an hour. Frequent copulation appears to be indispensible for continuous oviposition.

Oviposition.

At 20° C., after a preoviposition period of about two days the female starts laying eggs. She usually prefers an oviposition site that is neither very dry nor very moist. She turns around many times on the selected site, pressing the legs firmly to the surface making it rough and uneven. The genital " suckers " seemed to be pressed to the substrate while the eggs are being laid.

Oviposition continues for two to four weeks. A good deal of variation was discernible in the total number of eggs laid per female ; the range observed was from 459-1179 with an average of 738 eggs per female. The number of eggs laid per day also varied considerably, from 1-133, with an average of 34.5 eggs per day.

Rarely, the eggs hatch inside the female ; a state seemingly caused by blockage with consequent accumulation of eggs inside the body. Some of these eggs undergo normal development, but even after eclosion, the larvae remain inside the parent body for some time. The mother dies in these cases. A highly distented body with outstretched limbs fixed to the substrate and cessation of activity are indications of this internal hatching syndrome.

Associated organisms.

In the parent source of our experimental material, *C. anomalus* was seen with the anoetid mite *Histiostoma feroniarum*. The latter is a filter feeder and wallows in the semifluid part of the decaying material. There seems to be no biological associations between the two mites, and *H. feroniarum* died out in our stock cultures of the parent material with no apparent effect on *C. anomalus*. *C. anomalus* is seen sometimes on enchytraeid worm cultures where they might be subsisting on both the soil bacteria and the decaying worms. Macrochelid mites and nematodes were collected along with *C. anomalus* from decaying bulbs. The former are predators, but their effects on *C. anomalus* are not known.

Discussion.

C. anomalus passes through the same developmental stages as other hypopus-forming acarids, and the fecundity is very high in comparison with other acarids as Zakhvatkin (1941) showed for other members of the genus. 20°-25° C. seemed to be the optimum temperature for growth ; the maximum number of eggs hatched at those temperatures and the development from egg to adult is completed at a more or less even rate in 9-10 days. Schulze (1924) obtained similar results to ours with *C. berlesei* at 25°-35° C., but the period was lengthened to 28 days at 16° to 18° C.

The time taken to complete one generation is only about 12 days which fits well for habitats such as decaying substrates that can dry out rather quickly. Further, the larger the number of mites, the faster the substrates will be invaded by microorganisms upon which the mites feed. It is known that the mites introduce fungal spores and bateria into fresh areas of the host (Winston, 1956 ; Griffiths et al, 1959). Zakhvatkin (1941) cites that the mite excrement itself acts as a substrate for different bacteria. Thus the high fecundity and the fast rate of growth are of adaptive value.

The internal hatching of eggs, rarely noticed in *C. anomalus*, has been previously described in *C. moniezei*. Zakhvatkin (1941) mentions that in this latter species there are two kinds of females, one which lays a large number of eggs and the other a viviparous type characterized by a much larger size, distended hysterosoma and dull grey or brick red color. In the present study, females of *C. anomalus* with the internal hatching syndrome were found to have all the characters of the viviparous type described by Zakhvatkin. Furthermore, no other instance of polymorphism in females of acarids has been reported. It could therefore be suggested that the viviparous mites described by Zakhvatkin are gravid females with the internal hatching condition. The only difference in this respect between the observations made on *C. anomalus* and *C. moniezei* is that in the latter, females were sometimes found to contain not only larvae but protonymphs and even completely developed hypopi. In no instance has a stage beyond the larva been observed inside *C. anomalus*.

Summary.

The biology and behavior of *Caloglyphus anomalus* was investigated by culturing them in microcells on agar with Bonner's medium and *Escherichia coli*, at 100 % R. H. and at controlled temperatures of 15, 20, 25, 30, and 35° C. 20 and 25° C appeared to be near optimum, based on the average percentage of eggs hatched, 72.2 and 78.2 respectively, against about 50 % for the higher and lower temperatures. The life cycle was completed in 9.3 and 10 days on the average, while it was about 40 % longer at 15° and 40 % shorter at 30°. No hatching occured at 35° which was apparently lethal to the embryos. The life cycle comprised the egg, larva, protonymph, facultative hypopus, tritonymph and the adult. The morphology of the developmental stages including the hypopus has been described for the first time in this mite. *C. anomalus* has high fecundity, laying a total of 459-1179 eggs with oviposition lasting for 2-4 weeks. Occasionally the eggs hatch inside the mother, a conditon similar to that observed in *C. moniezei*.

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