

Bonn. zool. Beitr.	Bd. 47	H. 1–2	S. 77–86	Bonn, September 1997
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Post-eclosion heterochrony in the maturation of the adult females of a termitophilous fly (Diptera, Phoridae)

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Abstract. Many termitophilous adult insects postpone completion of the expansion of parts, such as the head and femora, until long after eclosion from their pupae. Consequently adults of different ages may differ markedly in appearance. Among the Termitoxeniinae the most extreme post-eclosion changes occur in the females of *Clitelloxenia assmuthi* (Wasmann 1902). Documentation of these changes lead to the proposal that five species be synonymised with this species. It has been argued (Assmuth 1913) that the females of this species are likely to ingest haemolymph from the older nymphs of their termite hosts. If so, ingestion of termite-nymph hormones might delay the cessation of expansion and sclerotization of parts of these flies following eclosion. At the least it is concluded that darkening of the cuticle cannot be treated as a reliable indicator of sclerotization. Probably darkening and hardening are decoupled in these flies.

Key words. Diptera, Phoridae, Termitoxeniinae, synonyms, heterochrony, teneral state, Isoptera, Termitidae.

Introduction

Heterochrony is the “dissociation, during development, of factors of shape, size, and maturity, so that organisms mature in these respects at earlier or later growth stages” (Nichols 1989). In evolutionary terms it has been defined as “an evolutionary change in the onset or timing of development of a feature relative to the appearance or rate of development of the same feature in the ontogeny of an ancestor” (Lincoln et al. 1982). It has evidently been a widespread mechanism giving rise to novelty during evolution (Matsuda 1987).

Among termitophilous insects heterochrony tends to manifest itself as a tendency for parts of certain adults to remain in the teneral state for a prolonged period after eclosion from the pupa. A general review of termitophilous insects (Kistner 1982) has shown that heterochrony occurs among termitophilous Carabidae, Cecidomyiidae, Phoridae, Scarabaeidae and Staphylinidae. In this paper a striking case of an Oriental species of Termitoxeniinae (Diptera, Phoridae) is documented and discussed.

This study has been made possible by my access to the extensive collections of termitophilous Phoridae made by Dr David H. Kistner (California State University, Chico) over many years. In addition I am grateful to the following for the loan of type material in their cares: Dr. H. Ulrich, Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn; Dr F. N. Dingemans-Bakels, Natuurhistorisch Museum, Maastricht; and Dr B. R. Pitkin, the Natural History Museum, London. I am grateful to my colleague Dr Simon Maddrell for useful discussions. My studies are currently funded by a grant from the Leverhulme Trust, to my colleague Dr William Foster for a Research Associate to work on termitophilous Phoridae, and the Isaac Newton Trust (Trinity College, Cambridge). I am grateful to W. M. Lee (Zoology Department, Cambridge University) for his skilled operation of the Scanning Electron Microscope.

Post-eclosion changes in Termitoxeniinae

The taxonomy of the aberrant termitophilous Termitoxeniinae, of the family Phoridae, is currently undergoing revision. This follows the realisation that the males, the flying-stage females and flightless-stage females had been erroneously assigned to three separate subfamilies by earlier authors (Disney 1989, 1990, 1992, 1994, Disney & Cumming 1992, Dessart 1993). It had long been recognised that the females undergo post-eclosion changes from a stenogastric to a physogastric stage (e.g. Assmuth 1913, Mergelsberg 1935). It has only recently been realised that the early stenogastric females shed their wing membranes on entering their host-termite's nest (Disney & Cumming 1992). Furthermore the procurement of mating pairs of an Afrotropical species has allowed reconstruction of the complete sequence of changes that occur in the adult females after eclosion. This has prompted a closer look at a taxonomically confused complex of six 'species' assigned to the Oriental genus *Clitelloxenia* Kemner, and a re-evaluation of these species in terms of most being different stages in a series of post-eclosion changes within a single species.

Clitelloxenia assmuthi (Wasmann 1902)

Termitoxenia assmuthi Wasmann 1902: 151. Holotype ♀, INDIA: Khandala, near Bombay (Natural History Museum, Maastricht) [presumed cotype material examined]

Termitoxenia peradeniyae Wasmann 1913: 20. Holotype ♀, SRI LANKA: Peradeniya (Natural History Museum, Maastricht) [examined]. Syn. nov.

Termitoxenia clitellaria Schmitz 1915: 36. Holotype ♀, SRI LANKA: Maha, Illupalama, Anuradhapura (Museum Alexander Koenig, Bonn) [examined]. Syn. nov.

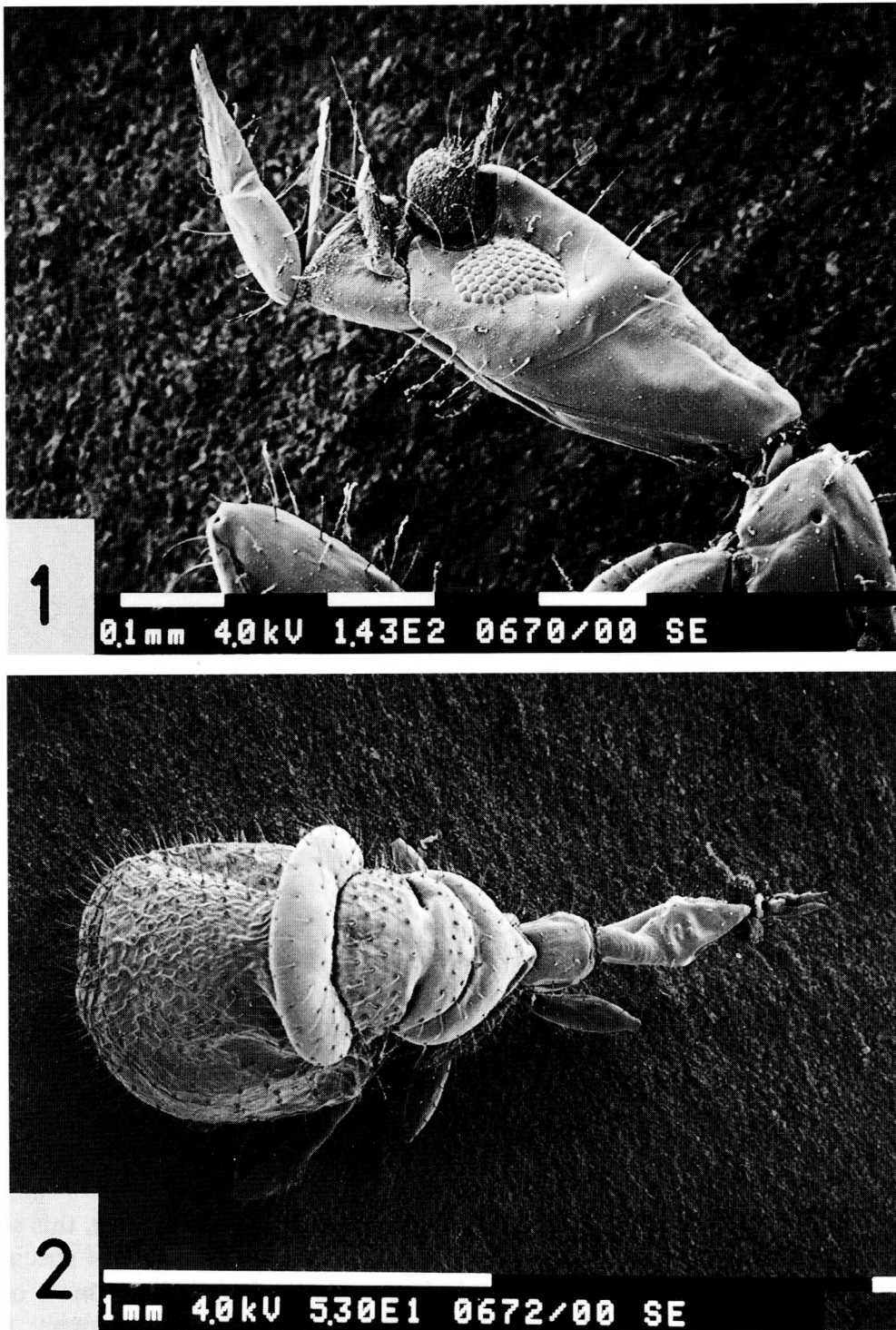
Termitoxenia longiceps Schmitz 1915: 36. Holotype ♂, MALAYSIA: Malacca (Natural History Museum, Maastricht — only two slide-mounted legs survive) [examined]. Syn. nov.

Termitoxenia hemicyclia Schmitz 1931: 176. Holotype ♀, JAVA, Buitenzorg (Museum Alexander Koenig, Bonn and also the Natural History Museum, London — a series of presumed cotypes) [series examined]. Syn. nov.

Clitelloxenia marshalli Schmitz 1938: 35. Holotype ♀, INDIA: Bangalore, Mysore (Museum Alexander Koenig, Bonn — one wing stump; rest in Natural History Museum, London) [examined]. Syn. nov.

A mature physogastric female from Java is shown in Figs 1 and 2. It is postulated that the material treated here as a single species exhibits a more marked degree of post-emergence change than most Termitoxeniinae. It is proposed that a failure to appreciate the extent of these changes in the females has misled early workers into describing as new species specimens which merely represented different stages of species already known. In most cases only limited material was available to these early workers. The larger samples now available, mainly because of the collections made by Dr David Kistner, serve to indicate that there are great differences between flies of different ages within a single sample, but little, if any, difference between flies of the same age from different samples. There is thus now no doubt that *C. clitellaria* and *C. marshalli* should be treated as synonyms. The small differences highlighted by Schmitz (1916, 1938) clearly lie within the ranges of variation to be found in a single sample of flies from the same termite nest.

The removal of two species by synonymy still leaves us with four 'species', which are based on geographical region — the Indian subcontinent, Sri Lanka, Java and Malaysia. Aggregated samples (of Kistner's material plus specimens in museums)



Figs 1–2: *Clitelloxenia assmuthi* mature physogastric female. 1, lateral view of head, 2, whole fly from above.

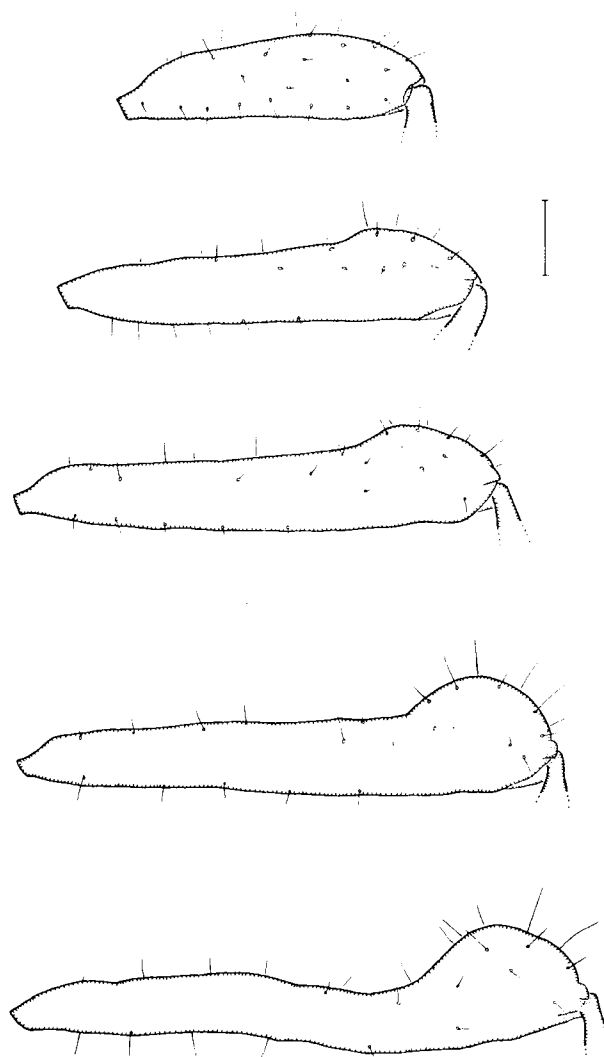


Fig. 3: *Clitelloxenia assmuthi* females, posterior faces of hind femora. The youngest fly at top and oldest below. (Scale bar = 0.1 mm).

from each of these four regions look different from each other. However, this seems to be primarily due to the different age structures of the total sample of specimens available for study from each region. Table 1 presents the length frequencies of the hind femora for females from the four regions. The differences between these aggregated samples for the four regions could be explained by any one of the following hypotheses:

- (1) An accident of sampling, such that the aggregated samples from each region happen to represent populations of different ages.
- (2) The four regions are characterised by four different taxa, species or subspecies, with different growth characteristics.

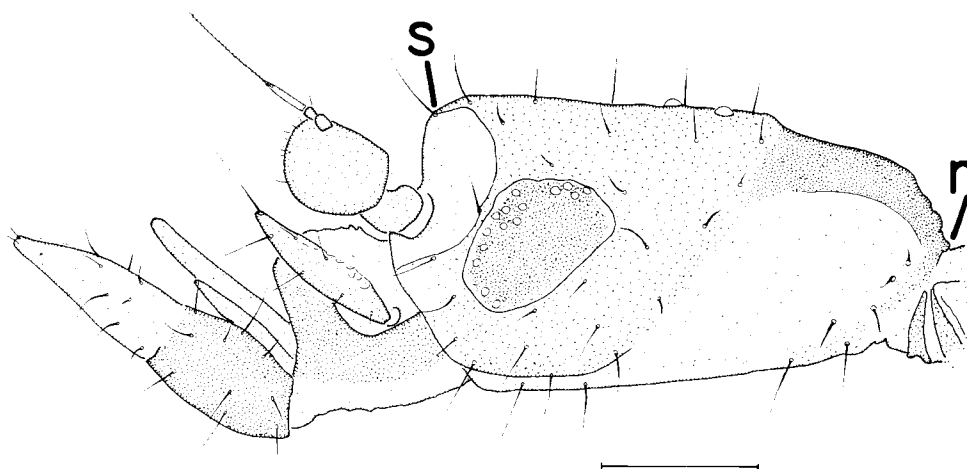


Fig. 4: *Clitelloxenia assmuthi* female, left face of head. s = anterior (lower) supra-antennal bristle; r = rear of head. (Scale bar = 0.1 mm).

(3) A single species is subjected to different phenotypic modifications of its growth characteristics in the different regions, possibly due to different species of *Odontotermes* serving as its hosts in the four regions.

The relationship between age of fly and length of hind femur is indicated by Fig. 3. This shows the hind femora of females from a single sample from a nest of *Odontotermes grandiceps* Holmgren from Bogor, Java (collected by Dr Kistner, 20 June 1977). The fly at the top had two developing eggs only 0.44 mm long, while that at the bottom had a single egg 0.93 mm long. In the topmost specimen the femur is only lightly tinged brown. In the bottom two specimens the femora are dark brown. Furthermore, as indicated by these two specimens, the larger the femur the more likely it is to exhibit distortion of its basic shape. Fig. 4 depicts the head of a female from Sri Lanka. The basiproboscis is seemingly well sclerotized and even more so the occipital region. Fig. 5 depicts the development of the occipital region in a series of females of the same series as for the femora depicted in Fig. 3. In Fig. 6 the ratio of the head length to length of hind femur is plotted for the 82 females of Table 1. The head length was measured from the anterior supra-antennal bristles to the back of the head (Fig. 4). Such a tight scatter of points, along a single straight line, would be highly improbable if the hypothesis of two or more sibling species were to be favoured, to explain the differences in Table 1.

Examination of slide-mounts of females made from the material collected by Dr Kistner, and the measurement of the lengths of the dominant developing oocytes in particular, has allowed certain inferences to be drawn. Typically two oocytes start to develop in the young stenogastric female. In a few cases both mature, eventually attaining a length exceeding 0.8 mm. Typically, however, one ceases to grow as the other starts to become more elongate (e.g. Fig. 7). The oocyte whose development is halted frequently proceeds to degenerate, but in some cases it seems to persist in a healthy but static state. Whether it will resume normal development when the first

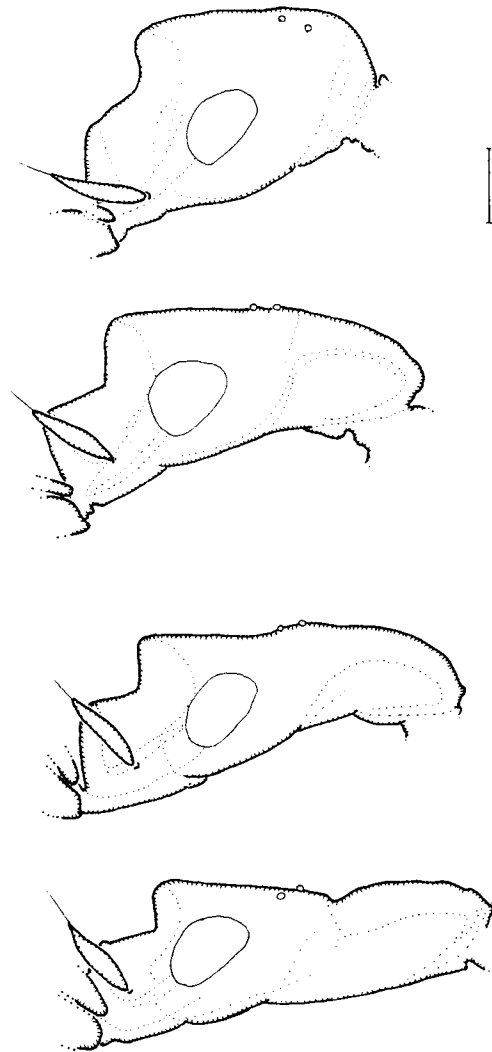


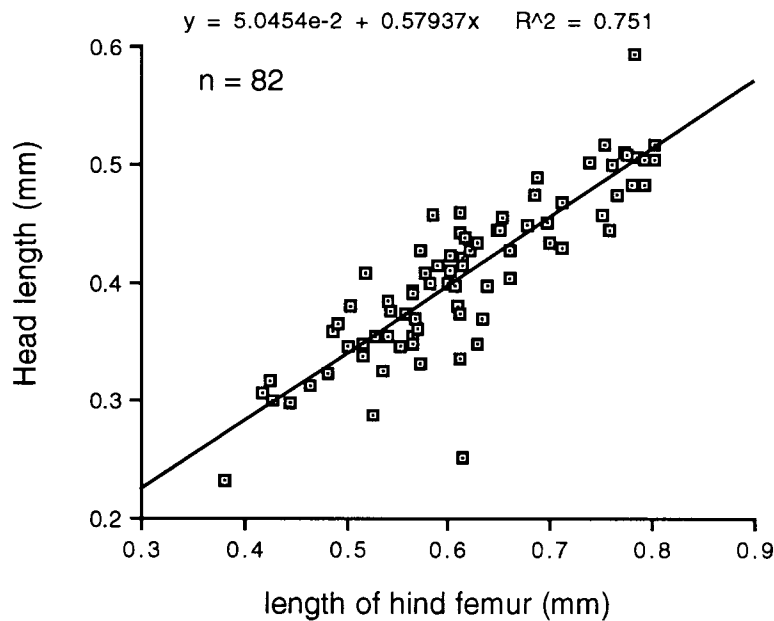
Fig. 5: *Clitelloxenia assmuthi* left faces of heads of females of different ages, the youngest at top (from the same series as in Fig. 3). (Scale bar = 0.1 mm).

Table 1: Recorded lengths of the hind femora of samples of females of *Clitelloxenia assmuthi* from different regions.

Region	length in mm					
	0.3–0.4	0.4–0.5	0.5–0.6	0.6–0.7	0.7–0.8	0.8–0.9
India + Pakistan	1	1	10	9	0	0
Sri Lanka	0	5	9	2	0	0
Java	0	2	9	16	4	0
Malaysia	0	0	0	1	11	2
TOTALS	1	8	28	28	15	2

Table 2: Recorded lengths of developing eggs in relation to lengths of hind femora of females of *Clitelloxenia assmuthi* from different regions.

Region	Femur length (mm)	length of developing oocyte (egg) in mm				n	$\frac{10x}{n}$
		0.2–0.4	0.4–0.6	0.6–0.8	0.8–1.0 (x)		
Pakistan	<0.6	1	6	5	1	13	0.8
Sri Lanka	<0.6	0	1	1	2	4	5.0
Malaysia	<0.6	0	0	0	0	0	0
Java	<0.6	0	0	0	0	0	0
TOTALS	<0.6	1	7	6	3	17	1.7
Pakistan	>0.6	0	0	1	4	5	8.0
Sri Lanka	>0.6	0	0	0	2	2	10.0
Malaysia	>0.6	0	1	1	11	13	8.5
Java	>0.6	0	2	3	8	13	0.62
TOTALS	>0.6	0	3	5	25	33	7.5

Fig. 6: *Clitelloxenia assmuthi* females, head lengths plotted against lengths of hind femora.

egg has been laid is not known. It needs emphasizing that when flies with oocytes and eggs of different sizes are arranged in order, from smallest to largest, then this correlates with the degree of differentiation of the egg. In flies with the shortest hind femora developing oocytes are not discernible in my slide-mounted specimens. In those with intermediate length femora the contents of the developing oocytes or eggs are little, if any, differentiated. In those with the longest femora not only has the

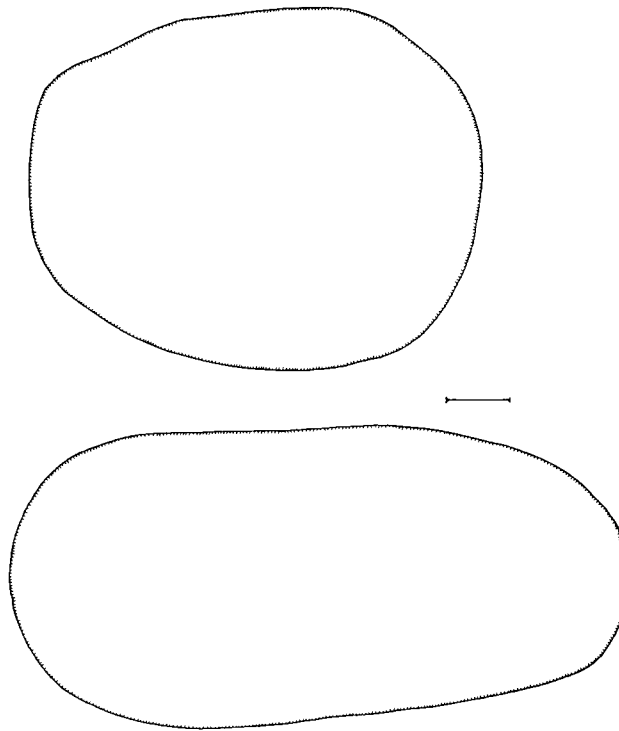


Fig. 7: *Clitelloxenia assmuthi* the two developing oocytes in a single female. The upper oocyte (of the left side) has ceased growing, the lower egg (of the right side) is nearing maturity. (Scale bar = 0.1 mm).

development of one egg halted, but in the other egg there is increasing differentiation of the contents, with the formation of an increasingly distinct chorion. The most mature eggs exhibit very little variation in length. Smaller flies do not have smaller mature eggs than larger flies, they have more immature eggs (which are therefore smaller) than are to be found in larger flies. In a few large flies no developing eggs could be observed. In these cases the appearance of the abdomen suggested that the lack of an egg was probably due to it having been recently laid. Measurements of developing eggs found are presented in Table 2.

The data in Table 2 provide no support for the hypotheses based on assuming that the females in the four regions have different growth characteristics. The most parsimonious conclusion, therefore, is that hypothesis (1) an accident of sampling, is sufficient to explain the differences between the samples from the four regions. Until defensible differences can be demonstrated, therefore, it is proposed to treat the material from the four regions as belonging to a single species, which continues to lengthen its femora and head right up to the oviposition of its first mature egg at least. Thus *C. peradeniyae*, *C. longiceps* and *C. hemicyclia* are herewith proposed as further synonyms of *C. assmuthi*.

Discussion

Clitelloxenia assmuthi exhibits the most extreme post-eclosion changes in the Termitoxeniinae studied to date. It is perhaps relevant to consider an inference proposed by Assmuth (1913). On the basis of the appearance of the gut contents and the structure of the mouthparts, he suggested that this species probably ingests haemolymph from older nymphs of its termite host. If so, such behaviour would ensure ingestion of hormones prevalent in the blood of these juvenile termites. These termite hormones might then serve to delay cessation of the expansion and sclerotization of the head and femora in these flies.

The continuing growth of the occipital region of the head in *Clitelloxenia assmuthi* after the apparent onset of sclerotization is most surprising. It is certainly evident that the darkening of the femora and occipital region is not correlated with a cessation of growth. At the least this suggests that darkening may be an unreliable indicator of sclerotization. The two familiar indicators of sclerotization, hardening and darkening, may not necessarily be coupled. Indeed it is established that sclerotization sometimes occurs without darkening, as in the case of albino insects (Chapman 1991). It is suggested that in these flies darkening is initiated earlier than hardening. If darkening and hardening are not decoupled in these flies then it would be necessary to postulate some reversal of hardening to allow continuing growth. This would seem most improbable.

Zusammenfassung

Bei manchen termitophilen Insekten wird das Wachstum von Körperteilen, wie Kopf und Femora, erst lange nach der Imaginalhäutung abgeschlossen, mit der Folge, daß Imagines verschiedenen Alters recht verschieden aussehen können. Was die Termitoxeniinae betrifft, wurden die stärksten postmetabolen Veränderungen der äußeren Gestalt bei den Weibchen von *Clitelloxenia assmuthi* (Wasmann 1902) beobachtet. Auf Grund von Korrelation und Häufigkeitsverteilung der Merkmale werden fünf weitere beschriebene Arten als Altersstadien von *C. assmuthi* gedeutet und mit dieser synonymisiert. Assmuth (1913) vermutete, daß die Weibchen dieser Art Hämolymphe von älteren Larven der Wirtstermite saugen. Sollte dies zutreffen, so wäre es denkbar, wenn auch unwahrscheinlich, daß der Abbruch des postmetabolen Wachstums und die Aushärtung der Cuticula durch Wirkung des aufgenommenen Juvenilhormons verzögert werden. Die Melanisierung der Cuticula setzt lange vor dem Stillstand des Wachstums ein und erfolgt demnach offenbar unabhängig von der Sklerotisierung.

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