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# Evidence from double infestations for the specific status of human head lice and body lice (Anoplura)

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ABSTRACT. Samples of head lice and body lice obtained from Ethiopians suffering from double infestations were mounted onto microscope slides and measured. The mean length of body lice (♀ 4.4 mm; ♂ 3.8 mm) was greater than that of head lice (♀ 3.5 mm; ♂ 2.9 mm), but the best discriminant was the length of the tibia of the middle leg (♀ 425/296 μm; ♂ 421/291 μm). No intermediate specimens were found in these double infestations, although intermediates can be produced experimentally by cross-mating. Since populations of head lice and body lice remain distinct it is concluded that they represent two distinct species, *Pediculus capitis* De Geer and *P.humanus* Linneaus.

## Introduction

The relationships between human head lice (*Pediculus capitis* De Geer) and human body lice (*Pediculus humanus* Linneaus) have several claims to our attention. The two forms are responsible for widely different problems of public health, though they are clearly closely related biologically. The question of the relative taxonomic status of these two taxa has been discussed repeatedly, without a convincing conclusion being reached (Ferris, 1935, 1951; Busvine, 1948; Schöll, 1955). Opinions range from that of Ferris, who described them as merely transient types of a polytypic species, to that of Freund (1924) and W. Eichler (1975, *in lit.*), who considered them to be separate species. Of considerable interest is the possibility that they represent species recently adapted to different sites on the same host, which is not uncommon in other genera of lice. In this case, the obvious connection with human loss of body hair and adoption of clothing, introduces an anthropological conundrum.

The purpose of this paper is to introduce some evidence of a kind not previously examined, namely the comparison of specimens from individuals with simultaneous infestations of head and body lice. Such double infestations are now rare in Europe though, according to Hase (1915), they were quite common in Eastern Europe some 60 years ago. At present in Britain, head lice are characteristically found on children, who are often quite cleanly in most respects; whereas body lice are mainly restricted to vagrants, often elderly and socially inadequate, who sleep in their clothes.

In double infestations, as pointed out by Keilin & Nuttall (1919), opportunities for interbreeding of the two forms may well occur; so it would seem of interest to discover how distinct they remain in these circumstances. An opportunity to investigate this followed a visit to Ethiopia, where double infestations are still quite common. Cmdr L. Sholdt, of the U.S. Naval Medical Research Unit No. 5, collected the specimens which were preserved in alcohol and later examined by me in London.

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## Material studied

*Series 1.* Small samples of adult lice were collected from the head and clothing of Ethiopians attending hospital in Addis Ababa. The patients were from various tribes (Table 1), and, except for one 14-year-old girl, all were young men. The imbalance of sexes was because fewer women had double infestations, but also because they were less willing for their hair to be shaved off. The weight of hair removed ranged from 14 to 40 g. The clothing, which was generally dirty, was largely of European type. However, most of these people wore a shamma, a toga-like garment which was 5–10 ft long, draped over the shoulders, arms and often the head.

*Series 2.* A smaller number of louse specimens was available from some remote villages in the south-west of Ethiopia. These were collected from tribes (Anuaks and Nuers) having little contact with foreigners. The people were largely unclothed but body lice were collected from bead necklaces and from the sleeping cloths used at night. The numbers of lice were low, but were adequate for the transmission of relapsing fever, which had been prevalent during the previous two years.

*Series 3.* These specimens had been preserved in 70% alcohol at the time of an earlier investigation (Busvine, 1948). They comprised head lice and body lice collected in London, but reared in captivity for thirty-three generations. They also included some of the $F_1$ hybrids of a cross between the two forms.

TABLE 1. Collections of human lice in Addis Ababa

| Host details | | | | No. of lice | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | In the hair | | | In the clothes | | |
| Age (years) | Sex | Tribe | Hair weight (g) | Total | Collected ♂ | Collected ♀ | Total | Collected ♂ | Collected ♀ |
| 19 | ♂ | Amhara | 16 | 51 | 2 | 3 | 56 | 1 | 10 |
| 14 | ♀ | Amhara | 40 | 918 | 10 | 8 | 1181 | 16 | 20 |
| 20 | ♂ | Gurage | 30 | 615 | 4 | 5 | 240 | 3 | 18 |
| 30 | ♂ | Gurage | 22 | 78 | 1 | 3 | 7700 | 8 | 22 |
| 26 | ♂ | Galla | 41 | 2167 | 4 | 24 | 10700 | 2 | 20 |
| 18 | ♂ | Gurage | 18 | 105 | 2 | 3 | 4900 | 0 | 20 |
| 19 | ♂ | Galla | 39 | 210 | 7 | 9 | 68 | 2 | 3 |
| 18 | ♂ | Amhara | 18 | 299 | 2 | 13 | 500 | 5 | 8 |
| 35 | ♂ | Amhara | 18 | 225 | 11 | 12 | 200 | 1 | 8 |
| 17 | ♂ | Galla | 14 | 45 | 5 | 4 | 700 | 9 | 12 |
| 23 | ♂ | Galla | 13 | 247 | 1 | 1 | 1300 | 12 | 12 |
| 25 | ♂ | Galla | 25 | 193 | 1 | 2 | 5200 | 6 | 12 |

## Methods

The most obvious character used to distinguish head and body lice is the gross size difference. Therefore measurements were made of total body length and also of the head and thorax. Whole lice were mounted in Faure's gum chloral medium on microscope slides and measured by a micrometer in the eyepiece of a dissecting microscope. Total body length, however, tends to be unreliable, because of the elastic nature of the integument. Well-fed lice are liable to have the abdomen extended telescopically, and the same effect can be produced by the pressure of a coverslip when the lice are mounted on slides. This unreliability is reflected in the divergence of mean values for both types recorded by different investigators (Table 2).

The various alternative measurements made by myself in the earlier (1948) investigation did not seem entirely satisfactory, in that all of them resulted in considerable overlap between small body lice and large head lice. I therefore took advantage of the parameters evaluated by Schöll (1955) and used the dimensions of the second pair of legs, which, according to his figures, give the greatest degree of discrimination (Fig. 1). To obtain these measurements a leg was cut off each louse and mounted in Faure's gum chloral. Because the legs were all slightly flexed they tended to lie on the slide in a uniform orientation; this helped to avoid errors of parallax. The sizes were measured by a micrometer in the eyepiece of a compound microscope.

The average tibial length of the second leg, according to my measurements for male lice, were 0.29 and 0.42 mm for head and body lice, respectively. These compare fairly well with Schöll's figures of 0.32 and 0.41 mm.



TABLE 2. Total mean lengths of head and body lice recorded by different investigators (in mm), with percentage differences

| Author | | Head strains | Body strains | % difference |
|---|---|---|---|---|
| Fahrenholz (1915) | ♂ | 2.56 | 3.23 | 21 |
| | ♀ | 3.10 | 4.20 | 26 |
| % difference | | 18 | 23 | |
| Busvine (1948) | ♂ | 2.68 | 3.32 | 19 |
| | ♀ | 3.18 | 3.81 | 20 |
| % difference | | 17 | 13 | |
| Schöll (1956) | ♂ | 2.96 | 3.99 | 25 |
| | ♀ | 3.69 | 4.51 | 18 |
| % difference | | 20 | 12 | |
| This investigation | ♂ | 2.91 | 3.79 | 23 |
| | ♀ | 3.55 | 4.42 | 20 |
| % difference | | 18 | 14 | |

## Results

The data were recorded separately for the various human hosts and examined for possible indications that some individuals had larger or smaller lice than others. No such trends were found, and therefore the measurements of lice from various hosts were combined according to origin (head or clothing) and sex. The mean body lengths of lice collected in Addis Ababa are set out in Table 3 and the measurements of parts of the middle leg in Table 4.

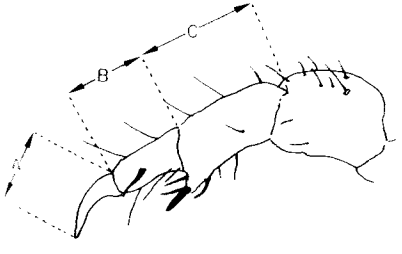


FIG. 1. Portions of the middle leg of the louse selected for measurement. A, claw; B, tarsus; C, tibia.

### *Sex comparisons*

It is well known that female lice are generally larger than males (cf. Table 2). From Table 3, however, it is evident that most of this difference is due to the larger abdomen of the female. In contrast, measurements of tibiae, tarsi and claws show no significant sex difference (Table 4), whereas the differences between head and body lice are highly significant ($P < 0.01$).

In speculating about these findings, one presumes that the larger abdomen of the female is required for the development of the ovaries, whereas the similarity of the leg and claw sizes may be due to the demands of the environment; those of head lice being related to grasping hairs.

### *Head louse/body louse comparisons*

The range of size, distribution and possible overlap of measurements of head and body louse populations can best be illustrated by histograms. Fig. 2 shows these data for the Addis Ababa lice and it will be seen that the

TABLE 3. Means (and standard deviations) of body length and parts thereof, of samples of lice from hair or clothing of Ethiopians (in microns); the per cent differences are based on the larger value in each case

| | Lice from hair | Lice from clothing | % difference |
|---|---|---|---|
| Head ♂ | 494 | 590 | 17 |
| Head ♀ | 522 | 656 | 20 |
| % difference | 5.3 | 10 | |
| Thorax ♂ | 685 | 850 | 19 |
| Thorax ♀ | 710 | 882 | 20 |
| % difference | 3.4 | 3.6 | |
| Abdomen ♂ | 1730 ± 107 | 2335 ± 146 | 26 |
| Abdomen ♀ | 2315 ± 154 | 2872 ± 234 | 20 |
| % difference | 25 | 19 | |
| Total ♂ | 2909 ± 155 | 3789 ± 138 | 23 |
| Total ♀ | 3548 ± 176 | 4415 ± 224 | 20 |
| % difference | 1.6 | 0.9 | |

TABLE 4. Means (and standard deviations) of portions of the mid legs of samples of lice from hair or clothing of Ethiopians (in microns); the per cent differences are based on the larger value in each case

| | Lice from hair | Lice from clothing | % difference |
|---|---|---|---|
| Claw ♂ | 214 ± 16 | 149 ± 9 | 14 |
| Claw ♀ | 211 ± 11 | 247 ± 11 | 15 |
| % difference | 1.5 | 0.8 | |
| Tarsus ♂ | 186 ± 9 | 239 ± 11 | 22 |
| Tarsus ♀ | 188 ± 13 | 244 ± 11 | 23 |
| % difference | 1.0 | 2.0 | |
| Tibia ♂ | 291 ± 18 | 421 ± 23 | 31 |
| Tibia ♀ | 296 ± 19 | 425 ± 19 | 30 |
| % difference | 1.6 | 0.9 | |

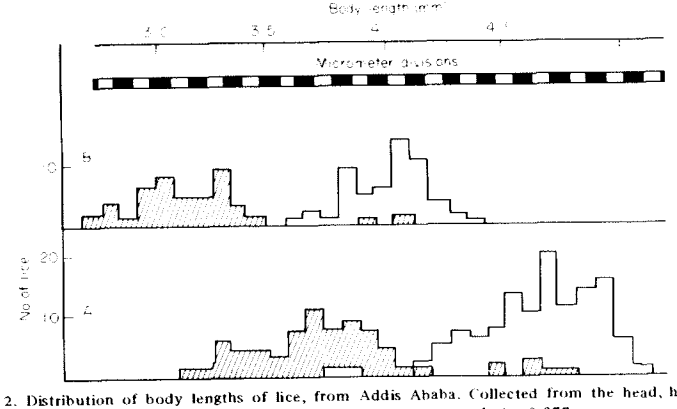


FIG. 2. Distribution of body lengths of lice, from Addis Ababa. Collected from the head, hatched; collected from clothing, plain. A, female lice; B, males. Micrometer scale 1 = 0.077 mm.



two forms remain remarkably distinct in these double infestations, with comparatively little overlap. There are, however, certain very distinct exceptions; notably two male and seven female lice found on heads, which fall well into the body louse range. All of these lice conformed in general appearance (colour and shape of abdominal segments) to the body louse type. In addition, there were two females found on clothing which fell into the head louse range but which conformed to the body louse type.

The mean measurements of the parts of middle legs of lice are given in Table 4. The most distinct separation of head and body louse types is given by measurements of the tibiae, while the difference in the tarsi is less and still smaller in the claws. This order of separation was also found by Schöll (1955), though to a less marked degree. His percentage differences for males were respectively 32.6, 29.3 and 25.8, as compared with 30, 22 and 14 in my results.

Because the measurements of tibiae provide the best discrimination between head and body forms, they were used for subsequent comparisons. Their distributions are shown by the histograms in Fig. 3. The lower diagrams (A and B) relate to the Addis Ababa lice, viz eighty-five males and 167 females taken from clothing and forty-three males and sixty-three females taken from hair. The general impression is an even sharper separation of the two forms than by body length measurements. The two female lice found on clothing, but falling into the length range of head lice, were found to have tibiae of normal (body louse) length. It is possible that their short length could have been due to immaturity, in contrast to the other lice which had well-developed ovaries. There remain, however, the nine aberrant specimens (two males, seven females) collected from hair, but falling into the body louse range. These were the same specimens noted as exceptions in the body length measurements.

It is interesting to note that similar findings apply to the smaller number of specimens collected from the Nuers and Anuaks (Fig. 3C). Again, the typical head and body louse measurements were widely separated (though both were smaller than the lice collected in Addis Ababa). Here again there were exceptions; more indeed, since head louse types were found on the body as well as body louse types on the head.

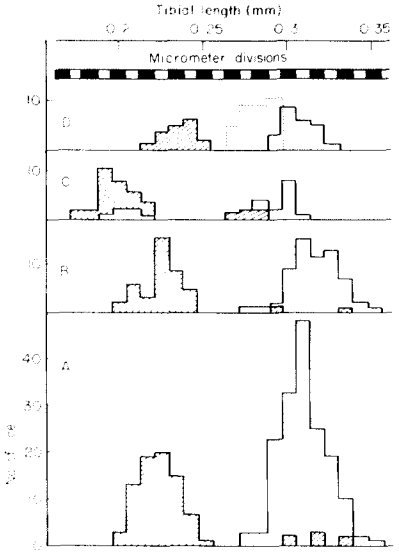


FIG. 3. Distribution of tibial lengths of lice. Collected from the head, hatched; collected from clothing, plain. A, female lice, Addis Ababa; B, male lice, Addis Ababa; C, lice from Anuaks and Nuers; D, lice from laboratory strains, with an $F_1$ cross indicated by a dotted line. In C and D, the sexes were combined. Micrometer scale 1 = 0.0115 mm.

It seems that the most likely explanation of the aberrant lice is that they were simply due to accidental contamination. In this connection, Cmdr Sholdt comments: 'We did nothing special as far as undressing the individuals. Their clothing was removed and their heads shaved as soon as they were admitted to hospital. Both men and women had to pull some article of clothing over the head to undress. If that article was heavily infested with lice, it is not unlikely that some lice might be transferred to the hair'. He also points out: 'The practice of wrapping the *shamma* about the head made me wonder early on if this might facilitate interbreeding on individuals with double infestations — especially as our surveys had shown *shammas* to be often heavily infested with lice'.

If, then, aberrant lice are evidence of mingling of the two forms of lice, they presumably offer the possibility of interbreeding: and since size commonly involves multifactorial inheritance, one might have expected to find intermediate forms. There does not seem to have been an adequate study of the inheritance of body and head louse characteristics, though my 1948 investigation provided some preliminary information. The progeny of (reciprocal) mass crosses between head and body strains were, in the $F_1$ generation, intermediate in mean size between the parents though somewhat nearer the body strain. As mentioned earlier, some of the these specimens were available for re-examination by the more reliable tibial length criterion (Fig. 3D). It can be seen that the dimensions of both parental stocks agree well with the recent specimens from Addis Ababa, and that the $F_1$ progeny are truly intermediate in tibial length, filling the gap between the parents.

## Discussion

### *Taxonomic status of head lice and body lice*

The results of these measurements of lice from double head and body infestations show that the two forms retain their characteristic size differences despite the fact that some body louse specimens were found on the head and that some head lice were found on the body (at least in the case of lice from the Anuaks and Nuers). It is known that the two forms will interbreed in the artificial environment of a pill-box and also that the $F_1$ hybrid progeny are intermediate in size. Therefore the absence of intermediate forms in the material studied is remarkable. Dobzhansky (1970, p. 357) says '... lack of "intersterility" in captivity or in an experimental garden does not rule out the possibility that reproductive isolation may be present in nature'. If some degree of such isolation exists, we cannot be sure to what it may be due. Keilin & Nuttall (1919) found hermaphrodites unusually common in hybrids between the two forms. I have not, however, encountered this in the present material, and even if this were a cause of reduce hybrid fertility it would not explain the absence of $F_1$ progeny. More probably the aberrant lice do not usually remain in the new environment long enough to breed.

The behavioural character which impels head lice to seek the scalp and body lice the garments is clearly a critical one, but little is known about it. Sikora (1917) mentions a case of body lice being put on the head of a man and subsequently being found in his underwear, and she herself conducted an experiment in which fourteen male head lice were put in the neck and shoulder region of a woman. Eight were later recovered from the hair (by combing) and the remainder lost. Still less is known about the mode of inheritance of this habit. Howlett (1917) recounted some tests done in India in which he and an assistant released some head lice in their clothing. These 'showed a distinct tendency to migrate to the head, and had to be put back again at intervals, but this character was markedly modified in their offspring, some of whom showed no definite tendency headwards. The eggs of these ($F_1$) individuals were mostly laid on clothing; a few (in my case) on the hairs of the body, but fewer than those on the clothing. In the next ($F_2$) generation the migratory tendency had very largely disappeared, and though a few individuals still showed it to some extent it was much less definite than in their grandparents. The majority did not show it at all. Chitinization and colour were also greatly modified in the *corporis* direction'. Howlett was writing 4 or 5 years after the actual experiment and it is not easy to assess these observations adequately in the absence of further details (nor do I know of any one eager to repeat the tests). They point, however, to the principle theoretical objection to according specific status to the two forms; that is the alleged 'transformation' of head lice into body lice. No one has claimed to have accomplished the reverse, but some similar changes have been observed in strains of lice reared in captivity, in pill boxes. Sikora (1917) was the first to report this about a strain sent to her from Warsaw by Rocha-Lima. Within three or four generations she noted a 22% increase of male body length and 37% in females. Keilin & Nuttall (1919) also briefly mention the same phenomenon in regard to samples of 'head' lice reared for 2 years by Bacot. More recently, Alpatov & Nastukova (1955) described extensive experiments with head and body lice collected from natural infestations and cultured in captivity which caused high mortality of the head strain. Extensive measurements were made of nine well-chitinized areas and these showed a steady shift towards dimensions of the body louse in the head louse colonies. Within five or six generations the change appeared to be complete.

In contrast to these investigators, others have found that head lice carefully maintained under similar conditions could retain their characteristic small size for six, eleven or even forty-three generations (Schöll, 1955; Sikora, 1944; Busvine, 1948; respectively). Mayr (1963, p. 464) seemed somewhat baffled by the fact that 'The findings and interpretations of various investigators, such as Busvine (1948) and Levene & Dobzhansky (1959), are in conflict with each other to such an extent that the existence of different genetic strains among head lice, and likewise among the body lice, must be assumed'. Most of the observations, however, can be explained by assuming that a limited amount of hybridization occurs in double infestations, or did occur in the past. It appears, however, that the gene flow is never enough to impair the distinct characteristics of the two forms. It follows, then, that some strains contain genetic characters of the opposite type; and this was probably especially true of colonies collected 60 years ago when double infestations were more common in Europe. When such mixed strains are reared in captivity there must be a constant selection for the body louse type, because all investigators agree that it is much more adaptable to artificial rearing than the head louse which suffers considerably more mortality.

It is, of course, very difficult to judge how much interbreeding occurs in nature, especially as this must vary from place to place according to the hygienic habits of the host. Under modern civilized conditions where, as I have pointed out, head and body lice tend to infest different types of people, isolation must be intensified. It is all the more interesting to find the degree of separateness in the specimens examined here, with evident opportunities for mixing; and these conditions must have obtained for a very long time prior to civilized hygiene.

Dobzhansky (1970, p. 313) points out that 'sympatric populations of sexual and outbreeding organisms must be isolated reproductively, for otherwise they could not keep apart and would fuse into a single population'. And again (p. 356) 'In contrast to races, species are able to maintain their genetic integrity despite sympatric co-existence'. On this basis, it seems not implausible to suggest that body lice and head lice should be accorded specific rank as *Pediculus humanus* L. and *P. capitis* De Geer.

In the discussion by Ferris (1951) the head louse body louse question is somewhat overwhelmed by the quite different question of geographical variants of human lice. These are based entirely on morphological data, often from very few specimens. They have not stood the test of sympatric co-existence like the head and body forms, which persist recognizably distinct all over the world. This fact would seem to be more important than the numerous small morphological differences which have been pointed out by various authors.

As I mentioned earlier, the public health status of the two forms is different. Head lice are more able to persist as a hygienic nuisance in civilized communities, but, unlike the body lice, they have never been incriminated as the essential vectors of typhus or relapsing fever. Furthermore, while strains of body lice resistant to organochlorine insecticides appeared in several countries from 1952, instances of resistance in head lice were not reported until over 20 years later.

### *Evolutionary speculations*

It seems reasonable to consider the head and body lice as a recent differentiation into two species inhabiting different parts of the same host. This presents special difficulties in evolution, as pointed out by Clay (1957) in regard to bird lice. 'It seems unlikely in the light of modern knowledge of genetics that sympatric speciation has taken place on the body of the bird, where there are no extrinsic isolating barriers, the plumage of one area grading into the next or in close contact with it. Even if the theory of conditioning is accepted, so that the Mallophaga hatched on the head and neck would tend to remain on that area, there would be nothing to prevent

interbreeding between individuals on the neck and those conditioned for the adjacent areas of back and wings. The presence of sympatric genera and species normally found amongst the Mallophaga can be explained by isolation and later re-union of parts of the louse populations ... and probably to a lesser extent by secondary infestations'.

The case of human lice is further complicated by being bound up with human loss of hair and adoption of clothing. It would be rash for me to speculate on the cause or even the sequence of these events, but it seems not unreasonable to suppose that they were in some way connected and, accordingly, roughly contemporaneous. It is conceivable then, that in one region the original hair-dwelling lice retreated to the scalp, while in another area they invaded the clothing. Subsequently, after a degree of differentiation, not involving complete genetic incompatibility, the human hosts of the two regions began to mingle and become infested with both forms.

A few additional remarks may be made on the causes of the size difference between head and body lice. Sikora (1944) plausibly suggested that the smaller size of head lice is advantageous in allowing them to slip easily through the dense hair of the scalp and escape capture, but I think she erred in ascribing the larger size of the body louse to better nutrition or a temperature difference. The latter is not great and, according to my 1948 data, it is slightly cooler in the hair which should result in larger specimens. In regard to nutrition, it could well be argued that the more robust body lice have been selected by the reatively adverse nature of their environment. Unlike head lice, which can feed at any time, they cannot feed while their host is active because of the shifting garments, and in some cases clothing is removed at night. Consequently, they tend to take fewer but larger meals. The 'pampered' head lice more readily succumb to starvation and are less adaptable to the unusual circumstances of artificial rearing.

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**References**

Alpatov, V.V. & Nastukova, O.A. (1955) Transformation of the head form of *Pediculus humanus* into the body form under changed conditions of existence. *Bulletin of the Moscow Natural History Research Society*, 60, 79. [In Russian].

Busvine, J.R. (1948) The head and body races of *Pediculus humanus* L. *Parasitology*, 39, 1.

Clay, T. (1957) The biting lice of birds. *Symposium on Host Specificity among Parasites of Vertebrates*. University of Neuchatel.

Dobzhansky, T. (1970) *Genetics of the Evolutionary Process*. Colombia University Press.

Farhenholz, H. (1915) Läuse verschiedener Menschenrasse. *Zeitschrift fur Morphologie und Anthropologie*, 17, 591.

Ferris, G.F. (1935) *Contributions towards a Monograph of the Sucking Lice*, viii. Stanford University Publications, California.

Ferris, G.F. (1951) The sucking lice. *Memoirs of the Pacific Coast Entomological Society*, 1, 1.

Freund, L. (1932) Anoplura. *Tierwelt: MittelEuropa*.

Hase, A. (1915) Beiträge zur einer Biologie der Kleiderlaus. *Flugschrift: deutsche Gesellschaft fur angewandte Entomologie*.

Howlett, F.M. (1917) Notes on head- and body-lice and on temperature reactions of lice and mosquitoes. *Parasitology*, 10, 186.

Keilin, D. & Nuttall, G.H.F. (1919) Hermaphroditism and other abnormalities in *Pediculus humanus* L. *Parasitology*, 11, 279.

Levene, H. & Dobzhansky, T. (1959) Possible genetic Difference between the Head Louse and the Body Louse. *American Naturalist*, 93, 347.

Mayr, E. (1963) *Animal Species and Evolution*. Harvard University Press.

Schöll, S. (1955) Kopf- und Kleiderlaus als Taxonomisches Problem. *Parasitologische Schiftenreihe*, Heft 1.

Sikora, H. (1917) Zur Kleiderlaus-Kopflausfrage. *Archiv fur Schiffs- und Tropenhygiene*, 21, 275.

Sikora, H. (1944) Meine Erfahrungen bei der Läusezucht. *Zeitschrift fur Hygiene und Infektionskrankheit*, 125, 541.

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# The egg, repagulum, and larva of *Byas albistigma* (Neuroptera: Ascalaphidae): morphology, behaviour and phylogenetic significance

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ABSTRACT. The external morphology and habits of the larval instars of the Central American ascalaphid *Byas albistigma* (Walker) are described for the first time, and its eggs and repagula (abortive eggs) are compared to those of a Brazilian *Byas* sp. described by New (1971). In most respects, all immature stages of *Byas* are shown to be much like those of another neuroptyngine (entire-eyed) owlfly, *Ascaloptynx furciger* (McLachlan). However, larvae of *Byas* are arboreal rather than terrestrial and possess a number of important morphological characters that are more primitive than those seen in *Ascaloptynx*. Shared features of the two genera that may constitute the ground plan of the Neuroptynginae are discussed in some detail and are weighted according to their primitive or derived status.

**Introduction**

*Byas* Rambur is a widely distributed Neotropical genus of strikingly large ascalaphids belonging to the 'entire-eyed' subfamily Neuroptynginae. It is thought to comprise only two species, although some recent evidence suggests that it should be placed in the larger genus *Haploglenius* Burmeister (Shetlar, personal communication). Other close relatives of the genus are *Ascaloptynx* Banks, *Amoea* Lefebvre, *Verticillecerus* Weele and *Episperches* Gerstaecker (Weele, 1908). All are badly in need of revision, as indeed are most owlfly taxa.

Recent studies of the Ascalaphidae have focused on the morphology and biology of the immature stages of selected groups (New, 1971; Rousset, 1973; Henry, 1972, 1976, 1977). In my studies I am attempting to reassess the evolutionary relationships of and trends within the higher taxa of Ascalaphidae using new data on positively identified immatures. The present paper represents an extension of these efforts to the genus *Byas*, for which no larva has previously been known. The eggs and larval instars of *Byas albistigma* (Walker), collected in Panama and reared in the laboratory, are described in detail with respect to both external morphology and habits. The significance of the work lies not so much in the characterization of an undescribed larva as it does in the formulation of the ground plan of immature Neuroptynginae for comparison with that of the better known Ascalaphinae. Toward this end, the larva of only one other neuroptyngine genus, *Ascaloptynx* Banks, has been positively identified and described (Henry, 1972, 1976, 1977). This form, together with the larvae of the six ascalaphine (split-eyed) genera known from the literature (summarized by Henry, 1976), will serve as the basis for comparison with *Byas* in the discussion.

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**Methods and Materials**

A gravid female was captured on 23 May 1976 'at light' on Barro Colorado Island, Canal Zone, Panama, by R. E. Silberglied and A. Aiello. I later identified this insect as *Byas*