NOTES ON *TUNGA CAECIGENA* (SIPHONAPTERA : TUNGIDAE)

BY

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NEOTUNGA EULOIDEA GEN. N., SP. N. (SIPHONAPTERA : PULICIDAE)

BY

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EDITOR'S NOTE

A FEW years before his death Karl Jordan prepared the manuscript of a paper on a Chinese Jigger Flea, *Tunga caecigena* J. & R., the female of which lives embedded in the skin of its host. After describing the extreme specialization of this species to its environment and contrasting it with free-living fleas, Jordan postulated the existence of a species in which the degree of specialization was intermediate between the two extremes. Recently material of a jigger-like flea, a parasite of pangolins in Southern Rhodesia, was received by Mr. F. G. A. M. Smit, who realised that in its specialization to a sedentary mode of life it accords very closely with the condition postulated by Jordan. This species is described for the first time by Smit on p. 365 below.

This striking fulfilment of Jordan's forecast is believed to justify the publication in this context of his manuscript which, though finished in draft, together with the relevant drawings, he never finally prepared for publication. Most of it, indeed, was left in his minute and barely legible handwriting, and but for Mr. Smit's skill and diligence in deciphering it, might never have seen the light of day. As it stands, the manuscript contains indications that Jordan would have wished to modify it, perhaps substantially, before publication. There are, for example, passages in which the author discusses the possible causes of the adaptations he describes, speculative essays of a kind which rarely, if ever, occurred in his published work. While in fairness to the author such passages have been omitted, and some necessary alterations have been made to clarify the original text, everything possible has been done to preserve its factual content and the author's characteristic style.

Mr. Smit has appended references to recent papers relating to the subject and has also made corrections to the figures where these were indicated in pencil by Jordan. The original manuscript and a transcript are in the Entomological Library, British Museum (Natural History).

SYNOPSIS

The modifications of intracutaneous fleas, as exemplified by a Chinese jigger, *Tunga caecigena*, are described. The existence of a flea showing a degree of specialization intermediate between that of the Pulicidae and that of the Tungidae is postulated.

Though the public is in general not very observant about the habits of such small creatures as insects, the flea has drawn attention to itself not only by the prick of its mouthparts, which is a mere fleabite, but particularly by the great nimbleness with which the tormentor evades capture. Agility varying in degree in different genera is indeed an almost general characteristic of the Siphonaptera, and whoever has tried to catch *Pulex irritans* will agree that this agility is a real advantage to the individual flea and therefore to the species. Nevertheless, in some 40 species not far removed in relationship from the human flea the female has given up this advantage and taken to a sedentary life, attaching herself to the host in a selected place until the end of her egg-producing existence. It is obvious that during the period of transition in the evolution from an agile flea to an immobile one the species had a bad time until new adaptions were perfected by natural selection, such as the strengthening of the exoskeleton or the evolution of the habit to settle in a place on the host where the parasite is comparatively free from destruction by tooth, beak or claw. New adaptations have more than made good the loss of the advantage of mobility, the sedentary fleas being so flourishing that at least some of them have become pests.

It is to be expected that the great step from agility of the female to immobility is associated with modifications in the morphology. These modifications are considerable, but in observing them we must bear in mind that the question of cause and effect implies opposite possibilities, either the change of habit in these fleas having been followed by morphological modifications or some profound morphological variation having caused a change of habit.

There are two kinds of sedentary fleas : the extracutaneous stick-fast fleas which fasten themselves to the host by the laciniae and epipharynx (which together form the piercing-sucking tube), and the intracutaneous jiggers or sand-fleas which live in a cyst within the skin of the host. In both kinds the males retain mobility, but are also morphologically greatly modified. The jiggers may be called either the most advanced or the most degenerate of all fleas both in body and habits. Extremes far transcending the average are always instructive and for that reason I have selected a Chinese jigger as an illustration of the changes to which I have alluded. The existence of this species was first mentioned by W. F. H. Blandford who, in 1894, gave an account of specimens sent to the Entomological Society of London from Ningpo (90 miles south of Shanghai). He rather doubted the flea to be identical with the common South American sand-flea (*Tunga penetrans*), described the expanded specimens and their situation in the ear of sewer-rats (*Rattus norvegicus*) and mentioned some differences from *Tunga penetrans*. When we wrote a monograph of the Sarcopsyllidae (Jordan & Rothschild, 1906) we asked Blandford for the loan of the Chinese specimens, but they could not be found. However, in 1920 he came across a slide, which he presented to N. Charles Rothschild and from which we described the species *Tunga caecigena* (Jordan & Rothschild, 1921 : 131). The species was redescribed as *Dermatophilus lagrangei* Roubaud in 1925[1] and in 1930 Wu described and figured the ear nodules and the flea contained therein. Of 250 rats obtained by Wu at Soochow 55 *Rattus rattus* and 13 *Rattus norvegicus* were infested ; the flea was identified as *Tunga caecigena* by Riley (1932). A number of years ago I had the pleasure of receiving from Dr. Teng Pin Hui, Director of the South Fukien Plague Station, the ears of 13 rats (*Rattus rattus alexandrinus* and *R. norvegicus*) preserved in formalin and all containing *T. caecigena* ; the rats were collected in Futsing, South

[1] Referred to as a synonym of *T. caecigena* by Sharif (1930 : 32).—F. S.

Fukien[2]. The consignment was most welcome, and I express here my sincere thanks to Dr. Hui and likewise to Dr. E. Landauer who had asked Dr. Hui to send the fleas to me. The total number of fleas in the 13 pairs of ears is nearly 190 (in various stages of postmetamorphic development), the highest number in one pair of ears being 31.

This series of specimens *in situ* enables me to supplement the previous accounts by describing in detail the growth and morphology of the adult female[3]. The internal morphology has only partially been studied ; that task is easier to accomplish with fresh specimens. . . .[4] All 190 specimens had entered from the ear's edge (Fig. 1). This restricted localization is interesting.[5] It is known of some agile species that they are found most frequently on definite parts of the body, one species for example on the neck and head, another on the rump ; the South American *Tunga caecata* (Enderlein, 1901), like the Chinese jigger confined to the ear of rats, enters the hind surface and not the edge. The female of *Tunga caecigena* arrives at the edge of the ear where it burrows into the skin and an environment is created in which it can safely accomplish the purpose of its life, the production of hundreds of eggs, each one of which is almost exactly as long as an unexpanded flea. The flea has only the laciniae and the epipharynx as implements for digging a hole. As the cuticle at the edge of a rat's ear is fairly thick, the flea—being only one millimetre long (Text-fig. 3)—will have disappeared inside before the sensitive portion of the skin is reached (Text-fig. 2*a*). . . . [6] In the large cysts containing specimens with the frontal end of the swollen abdomen projecting forward as four large humps, the bottom of the cyst shows the impression of the four humps and of the hole into which the mouth-parts were inserted : a mould of the anterior end of the flea. The only connection with the outside is the hole by which the flea originally entered, the aperture growing larger with the flea, and the only part of the flea in contact with the atmosphere is the tail end which is but slightly below the surface of the skin of the host.

Among the fleas found in ears sent by Dr. Hui are a number of specimens of different sizes and appearance. In many of the rats' ears the cysts are so closely packed that they interfere with each other, thus apparently affecting the growth of

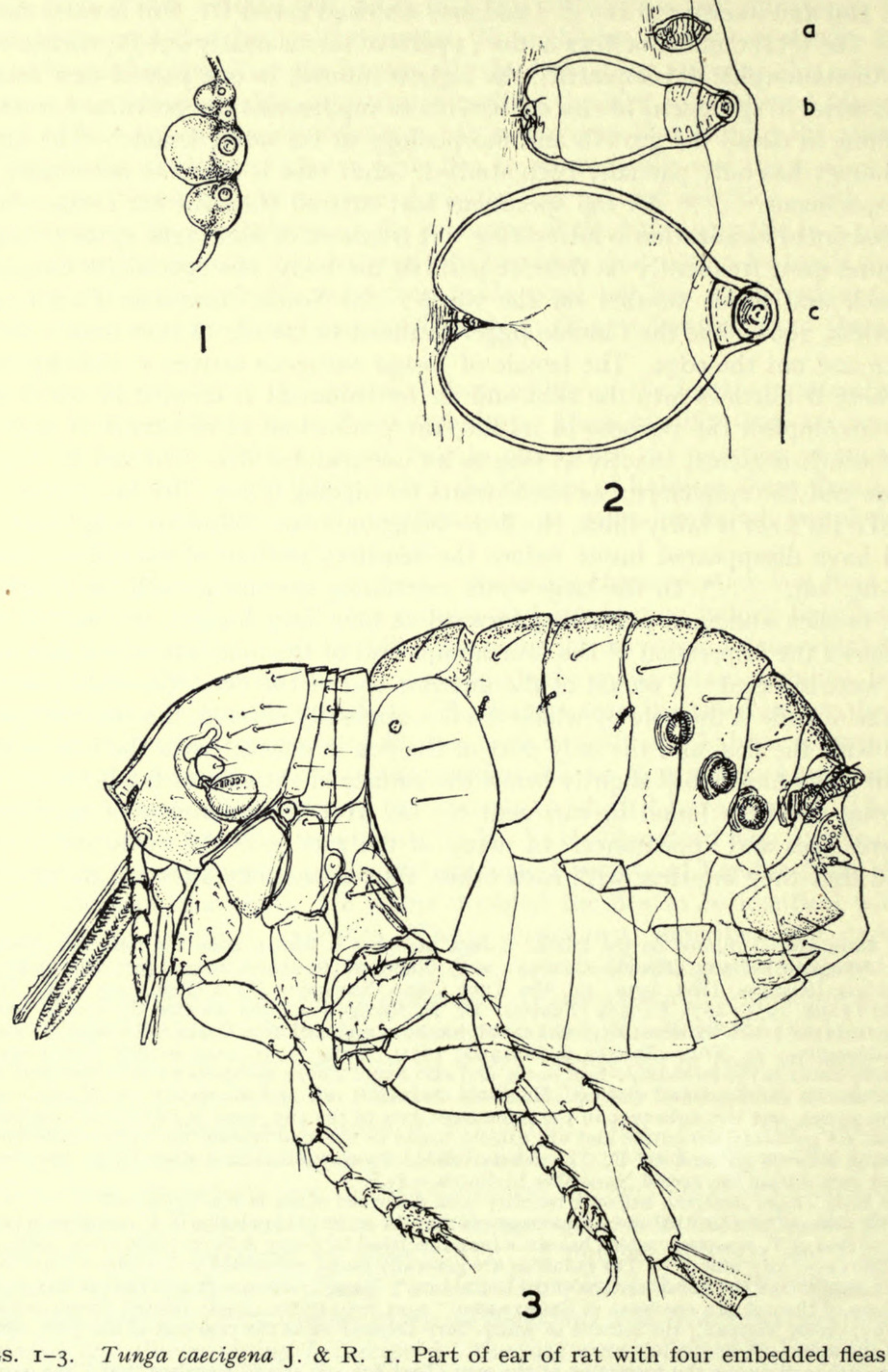
[2] No dates are mentioned on the labels. *Tunga caecigena* is known from the following localities in China : Ningpo (Chekiang) (Blandford, 1894 : 229), Shanghai (Roubaud, 1925 : 401), Dong Chia Hong, nr. Soochow (Kiangsu) (Wu, 1930 : 59), Wu Tung Chiao (Szechuan) (Li & Chin, 1957 : 120), Foochow (Fukien) (Yang, 1955 : 287), Futsing (Fukien). Dr. K. Sakaguti informs me that the species was introduced into Japan probably about 1940 and that it has been reported from Osaka (Morishita & Arai, 1949) and Nishinomiya, nr. Kôbe (Tanaka & Ikuzawa, 1951). Yang (1955 : 293) records *Rattus norvegicus* and *Rattus rattus* as the most important hosts, and also found *Tunga caecigena* on *Mus musculus*, *Suncus murinus* and an undetermined wild rat. He states that adult rats and shrews are more heavily infested than the young, and the difference in the infestation rate of the two sexes is statistically insignificant. The fleas are probably univoltine and are usually found in the cold season, the optimum temperature zone being between 50° and 60° F. The closely related *Tunga callida* Li & Chin, 1957, also, has been collected only during the period November to March.—F. S.

[3] The male *Tunga caecigena* has only recently been described (Chen & Ku, 1958).—F. S.

[4] In the passage here omitted the author suggests that the mode of copulation in *T. caecigena* is probably similar to that of *T. penetrans*, which has since been described by Geigy & Suter (1960 : 207, 208).—Ed.

[5] Yang (1955 : 293) states : " The parasites are generally found embedded at the edge of the rats' ears, but they may attack the dorsal surface of the hosts' ears." Yang's reference that " Once it was also found at the base of the tail of a specimen of *Rattus rattus* " may refer to the closely related *Tunga callida* Li & Chin, 1957 (from Yunnan), the females of which bury themselves at the rear end of the host, especially around the anus.—F. S.

[6] The author discusses the formation of the cyst (Text-figs. 2*b*, *c*) and surmises that " the expanding flea moulds the cyst and not the cyst the flea ".—Ed.



FIGS. 1–3. *Tunga caecigena* J. & R. 1. Part of ear of rat with four embedded fleas in various stages of postmetamorphic growth. 2. Cross-section of skin of rat's ear, showing embedded fleas in (*a*) the first stage of postmetamorphic growth, in (*b*) an intermediate stage and in (*c*) the final stage. 3. Whole female, cf. Fig. 2*a*.

some specimens. Though we have no proof that each individual of this flea goes through all the stages observed before it reaches its final shape and size, the evidence points in that direction. Text-figs. 4–10 represent these stages. The exoskeleton is almost intact in Text-fig. 4 ; in Text-fig. 5 the expansion of the abdomen has begun ; in Text-fig. 6 the membrane between terga I and IV is greatly extended and at segments II and III there is a constriction ; in Text-fig. 7 the anterior swelling between segments I and II already conceals part of the thorax and the second constriction has shifted backwards ;[7] in Text-fig. 8 a small swelling appears all round the thorax, a sort of cushion on which lie the thorax and head ; Text-fig. 9 shows a fully distended female in which the anterior swellings, two each side, completely conceal the head and thorax in lateral aspect[8] but they are visible in a view from the front or slightly askew (Text-fig. 10).[9]

I have taken about half the number of specimens out of their cysts, and left the others *in situ*. Most specimens have attained full size or nearly, but about 20 are small and look to me as if they represent the first stages in the individual growth from the non-expanded female to the fully expanded one. The smallish specimens vary a good deal in shape and this may partially be due to overcrowding.

The exoskeleton of an adult insect, being a finished product, does not grow any more and is not affected, apart from degeneration, by the expansion of the volume of the body necessitated in many female insects by the development of the great number of comparatively large eggs in the abdomen. Head, thorax and their appendages are the same size in the unexpanded jigger female (Text-figs. 2*a*, 3) as in the fully expanded specimen of over 8 mm. (Text-fig. 2*c*). However, the life in the cyst has a remarkable effect on the legs in jigger fleas, the tarsi, tibiae and femora disappearing partially or completely, the process beginning with the hind tarsi (cf. Wagner, 1932 : 249). In the series of some 90 specimens of the Chinese jigger only a few have one complete tarsus, and not a single one has a complete hind tarsus.[10] Only the first segment is preserved in the hind leg of one specimen and this exhibits strong signs of degeneration (Text-fig. 3).[11] . . . [12] This process seems to set in soon after the skin of the host is entered, for the unexpanded and only slightly expanded specimens (Text-figs. 4–6) have already lost all tarsi. The small degree of expansion in these females, however, may be due at least partially to overcrowding.

The enlargement of the abdominal cavity is made possible by the postmetamorphic growth of the intersegmental membranes as in all adult insects with secondarily enlarged abdomen, such as the queen termite, the oil-beetle (*Meloë*), and repletes of honey ants. But the growth of the jigger female differs essentially in the abdomen being transformed into a different shape, affecting the function of the segments,

[7] This figure closely resembles that given by Yang (1955 : fig. 1).—F. S.

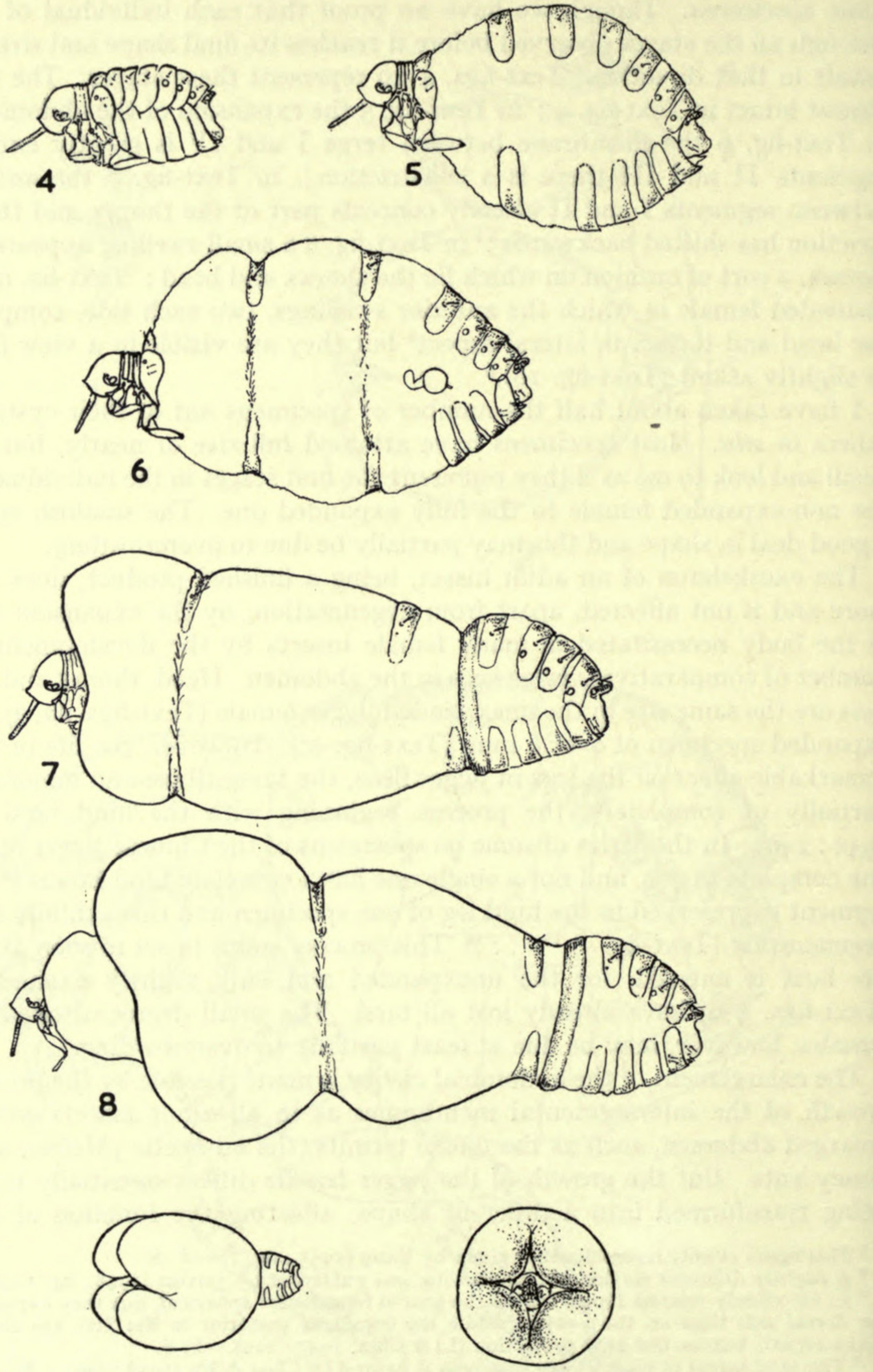
[8] A slightly different version of this drawing was published by Jordan (1948 : fig. 129D).—F. S.

[9] In the closely related *Tunga callida* the gravid females are spherical, but they expand much more on the dorsal side than on the ventral, while the segments posterior to the fifth are elevated to form a characteristic button-like anal projection (Li & Chin, 1957 : 120).—F. S.

[10] The hind tarsus of male *Tunga caecigena* is figured by Chen & Ku (1958 : figs. 1, 8).—F. S.

[11] Some species lose parts of their legs more readily than others, *e.g.* in embedded females of *Tunga penetrans* the legs are usually all intact, even in the final stage of expansion. Are parts of the legs lost in certain species during the act of burrowing into the skin ? If those parts are shed after this process one would expect to find remnants in the cyst.—F. S.

[12] The author suggests possible reasons to account for the loss of parts of the legs.—Ed.



FIGS. 4–10. *Tunga caecigena* J. & R. in various stages of postmetamorphic development; explanations in text. (Actual size of specimen shown in Fig. 4 : 1 mm.; in Fig. 5 : 2 mm.; in Fig. 6 : 2·6 mm.; in Fig. 7 : 3·4 mm.; in Fig. 8 : 5 mm. Figure 8 drawn to a somewhat smaller scale than Figs. 4–7 ; Figures 9 and 10 drawn to a much smaller scale.)

segments I, II and III becoming merely an expanded container and IV–X being consolidated into a tough truncate cone and serving as the only connection of the parasite with the outside world. It is a teleomorphosis of form affecting function.

As will be evident from a comparison of Text-figs. 5–7, the intersegmental membrane between tergites I to III and between thorax and sternites II and III (there is no sternite I in fleas) are the first to grow longer and expand all round, tergite I remaining attached to the thorax. In Text-fig. 7 tergites II and III have travelled backwards, and a tough belt is formed in front of the two sclerites of segment IV, the specimen being here constricted and remaining so ; the anterior part of the abdomen has swollen forward. In Text-fig. 8 the head and thorax are on a cushion-like swelling, which later on becomes smaller—the specimen is still constricted at segment II. Further expansion breaks the constriction at segment II and the swelling extends far beyond the head, forming anteriorly on each side two dome-shaped projections, one tergopleural, the other sterno-pleural (Text-fig. 9) ; the slits between these four humps form an erect cross (Text-fig. 10) ; in a frontal view the head and thorax are seen deep down in the centre of the cross. The four humps are not always of equal width and length, but are always present in expanded specimens, being a specific distinction of the Chinese jigger.[13] Among the American species, *Tunga terasma* Jordan, 1937, likewise has four humps, which, however, are directed sideways, somewhat in the manner of the arms of an X, the head and thorax not being concealed.

After the formation of the belt (Text-fig. 7) in front of the sclerites of segment IV, the anal cone undergoes very little change. The tergal plates are well separated from the sternal ones and their dorsal and ventral parts, respectively, often show stronger chitinization. The cone is firmer than the enlarged part of the abdomen, which is chiefly due to the large number of muscles which extend from the segments of the cone forward to the thorax. The cone varies slightly in length, being shorter in some specimens than in others. In a view from behind the cone is occasionally surrounded by a brown ring formed by the faeces (remnants of the blood of the host) as in females of other species of *Tunga*. The exposed area encircled by this brown ring appears often to be lower than the margin of the aperture in the host's skin and has erroneously been termed a cloaca by various authors. As in all fleas, the rectum and the oviduct have separate orifices, the anus being situated between the tergite and the sternite of segment X and the oviduct opening between sternites VIII and IX.

The majority of female Tunginae have no distinct line of demarcation between tergites IX and X, the two segments being fused. In a lateral view (Text-fig. 12) the triangular sclerite projecting backwards from the sensilium represents the tergum of segment X and the lateral short projection with a long apical bristle the tergopleurite homologous to the stylet present in the large majority of fleas ; below this pleurite there is a separate narrow sclerite bearing some bristles which is sternite X. In a view vertically on to the terminal surface of the cone (Text-fig. 13) sternum X appears as a narrow transverse bar bearing right and left a pair of bristles ; the apex of the combined tergites IX and X is deeply sinuate and the backward projection each side of the sinus is much foreshortened ; the anus is situated above sternum X.

[13] See footnote 9.

The midgut of swollen and large specimens is folded twice, thus being divided into three parts as shown in Text-fig. 11.[14]

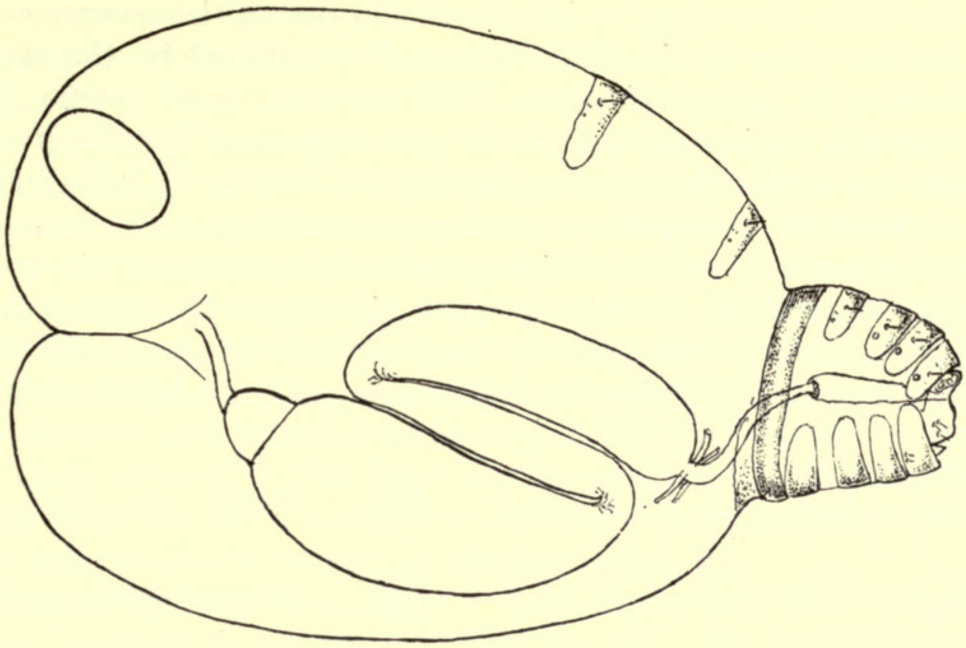
A problem which has remained obscure to me concerns the means of transporting the eggs from all parts of the large abdomen to the oviduct. Schimkewitsch (1884 : 673) found only two longitudinal muscles in *Tunga penetrans*.[15] Though the number of muscles is much larger in the Chinese jigger, I do not see how, in fleas which are often placed in the ear with the head downwards, the longitudinal muscles can guide the eggs from the anterior humps upward to the anal cone without the co-ordinated help of the transverse or ring muscles.[16] However it may be accomplished, eggs do arrive in the oviduct and are ejected. As the transverse diameter of the ripe egg is much greater than the diameter of the oviduct, the passage of the eggs is only possible because the structure of the anal cone admits considerable expansion in width. The two segments chiefly concerned in the process of egg-ejection are the tergite and sternite of segment VIII and the sternite of segment IX. Tergite VIII is divided dorsally in the median line into a right and left sclerite, which extend downward to or near to the ventral surface of the abdomen. Other tergites are not halved (the apical margin of tergite VII is in some specimens slightly or more deeply incised medially). From the spiracle downwards tergite VIII widens considerably and in unexpanded specimens the lower areas of the right and left halves approach one another ; on the outer surface of the lower area there are three or four bristles and on the inner surface about half a dozen directed inward-distad (Text-fig. 13 ; the two halves are drawn as they appear in the specimen, the left half being more flattened and expanded in the preparation than the right half ; Text-fig. 12, lateral aspect). Sternite VIII lies in between the two halves of tergite VIII ; it differs much from the corresponding segment of the American jiggers[17] by being soft and tough, and ends in a pointed sclerotized cone. Below and in front of it lies sternite VII (Text-figs. 12, 13), which is divided medially and bears right and left two bristles, sometimes one. At the side of sternite VIII are two humps, flexible like the main body of st. VIII, and above the sternum is the orifice of the oviduct. The upper wall of the terminal part of the oviduct is formed by a large sclerite homologous to sternum IX and this is a special feature of the species of Tunginae. This sclerite extends from the ventral margin of tergite IX downward, forming a kind of half cylinder resembling an elastic plate or a piece of paper of which two opposite margins are bent towards each other. The cavity thus formed is closed on the frontal side by the intersegmental membrane connecting sternum IX with X. The pressure exercised on the egg by the muscles of the abdomen will push the egg to the end of the oviduct where it is held between sterna IX and VIII and the stiff bristles on the inside of the right and left halves of tergite VIII. The egg pressing against the convex surface of the elastic sternum IX, bends this

[14] In fully distended specimens of *Tunga penetrans* the midgut is folded four times (Geigy & Herbig, 1949).—F. S.

[15] Geigy & Herbig (1949) found, apart from the hemispherical muscles, only one central muscle cord in the abdomen of inflated specimens of *Tunga penetrans*.—F. S.

[16] It would seem that the pressure inside an ovariole, caused by the process of egg-growth, is sufficient to push the eggs forward till they reach the oviduct, whence the exertion of muscular power will be necessary only for the ejection of the eggs.—F. S.

[17] In female *Tunga penetrans* sternum VIII appears to be entirely membranous ; I have not been able to detect it in any mounted specimens.—F. S.



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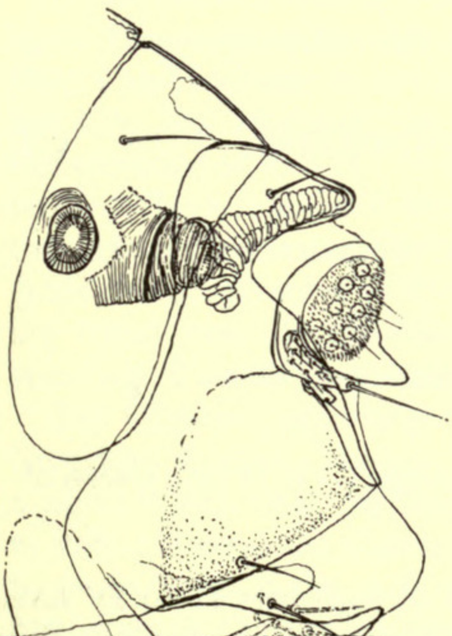

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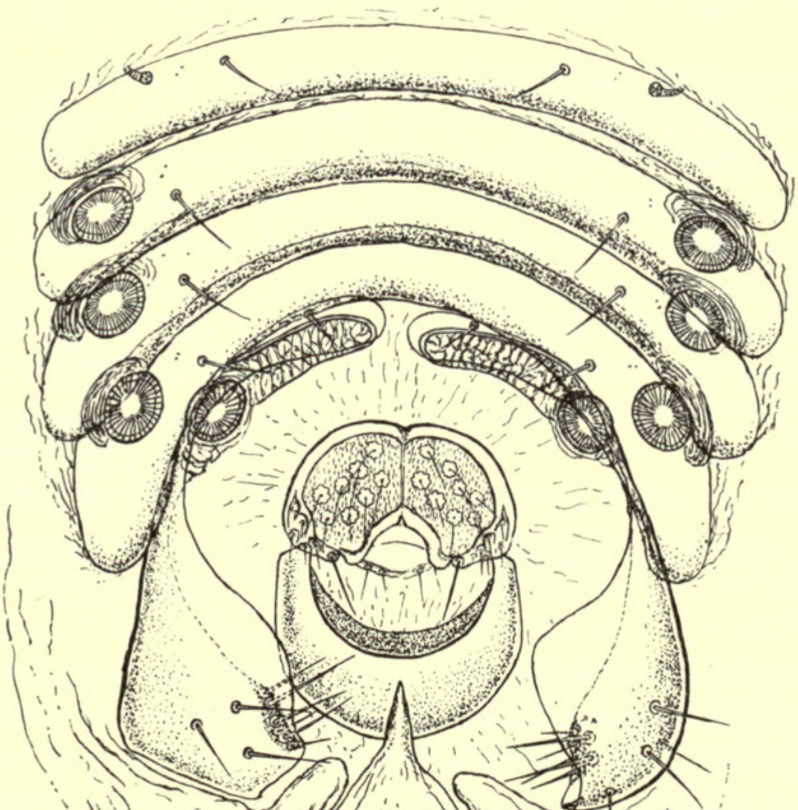

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FIGS. 11–13. *Tunga caecigena* J. & R. 11. Flea in final stage of expansion, showing alimentary canal and a full-sized egg in upper left part of abdomen. 12. Terminal abdominal segments of female in lateral view. 13. Same segments as viewed from behind.

surface upward (there is an egg in this position in one of the specimens of this flea) and now a further effort of the muscles would be assisted by the elastic force of sternum IX and of the bristles of tergum VIII and achieve the ejection of the egg.

The third function of the anal cone is the provision of air for the greatly enlarged abdominal tracheal system by means of enlarged spiracles. Spiracles, as part of the exoskeleton, cannot be enlarged by postmetamorphic growth of the individual; their enlargement can only be due to the result of the evolution of the species. In the process of postmetamorphic growth, however, shifting of the segments bearing the enlarged spiracles has kept the posterior four of them (on segments V to VIII) in contact with the atmosphere, whereas the anterior series are in the cavity and there-

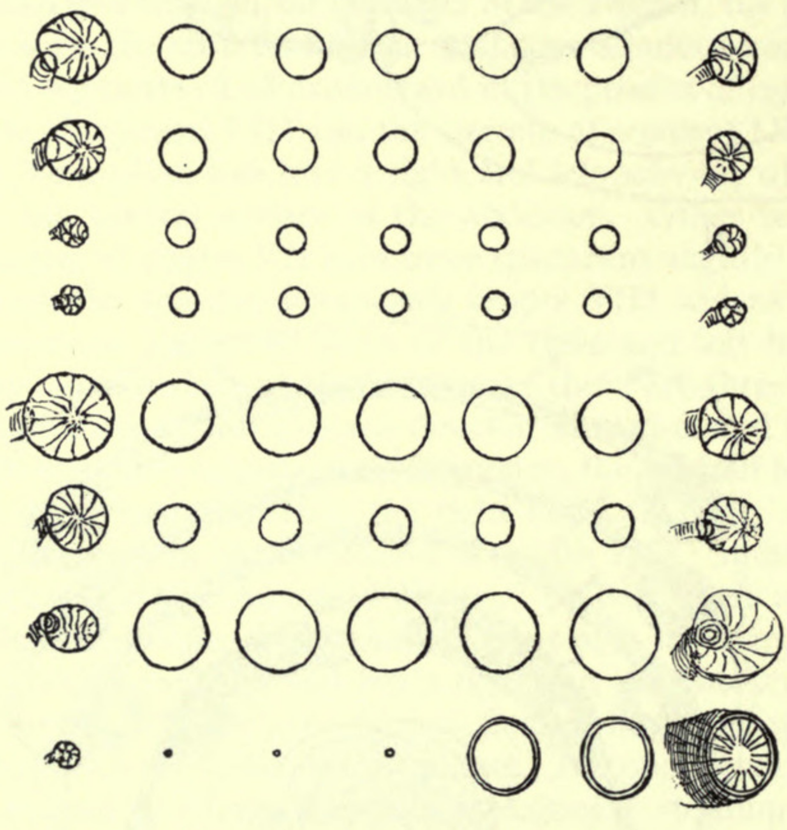

FIG. 14. Abdominal spiracular fossae of metepimeron and terga I–VII of four species of Pulicid fleas.

fore shut off from the atmosphere. The three spiracles of segments II to IV have hitherto been considered absent. If they were as minute in the Chinese jigger as they are in *Tunga penetrans*[18] I should very likely not have discovered them. Nature has provided two guides with the help of which the vestiges of these spiracles can be found, provided the process of clearing the specimens for the balsam preparation has not altogether destroyed the trachea of which the spiracle is the aperture. The guides alluded to are a bristle and a pair of minute dots [leucodiscs]. The abdominal terga I–VIII of the jiggers, inclusive of the male of *T. penetrans*, each has one subdorsal bristle. That this bristle is present on segment VIII is contrary to what one would have expected, there being no bristle above spiracle VIII in any of the fairly numerous

[18] I have failed to detect vestiges of spiracular fossae on terga II–IV in mounted female specimens of *Tunga penetrans*.—F. S.

species of the group of Siphonaptera to which *Tunga* must be assigned, whereas one or more bristles are present above the stigma of VIII in many species of other groups of fleas with which *Tunga* is much more distantly related than for instance with *Hectopsylla*. Nor can I look upon that bristle as a character which was lost in the ancestors of the Tunginae and has reappeared. The development of the bristle on tergite VIII is most probably due to isomerism, a detail repeated on every segment. However that may be, a little more downward and forward from the bristle there are two transparent dots, sensory cups, and below these we find the vestigial spiracle (Text-fig. 3). The somewhat larger size of the remnants in the Chinese jigger may be taken as evidence that there have existed—and possibly there still exist—species in which these anterior abdominal spiracles approached the size of the first abdominal one (on the metepimeron).[19] That is to say the reduction of spiracles II–IV and the compensating enlargement of spiracles V–VII took place gradually or step by step. Is there any other evidence bearing on this suggestion ?

A comparison of the male spiracles of *T. penetrans* proves that this process in their evolution was confined to the female (Text-fig. 14) ; the series of rings, drawn to scale (spiracle of tergum VIII omitted), shows neither reduction in II–IV nor enlargement in V–VII ; the first spiracle, on the metepimeron, is the same size as the following ones.

In the male of Hectopsyllinae (Text-fig. 14) the proportional size of the spiracles is again the same as in male *T. penetrans* ; in all females, however, II–VII are larger than I and increase in size from II to VII. The Hectopsyllinae and the Tunginae are the only fleas in which the abdominal spiracle I of the female is much smaller than the spiracles of V–VII ; in all other fleas spiracle I is as large as the following ones or larger. This evidence of the existence, in the female of the Tungidae, of a disposition toward the evolution of enlarged abdominal spiracles explains the exceptionally great size of spiracles V–VII in the jigger females. No other fleas show a corresponding trend towards the elimination of spiracles II–IV. The degeneration of these spiracles, therefore, must be attributed to the loss of function.

The Chinese jigger is in some respects of a more generalized type than the five American species of *Tunga*. It is therefore not far fetched to assume the existence of a jigger which only partially enters the skin of the host. We should expect to find in such a species the abdominal spiracle II in the process of degenerating, III and IV to be perhaps of the same size as in the male and V–VII more or less enlarged : a first step in the modification of the spiracles.[20] It may be left to the imagination of the reader to reconstruct the further steps to be passed before the evolution of the jigger females as we now know them.

[19] There is now one such species known ; see below, p. 375.—F. S.
[20] See footnote 19.

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