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THE MYSTERY OF THE SO CALLED "TRILOBITE LARVAE" OR "PERTY'S LARVAE" DEFINITELY SOLVED.¹

BY ERIC MJÖBERG.

CONTENTS.

I.	Introduction.....	119
II.	Historical.....	120
III.	New Investigations.....	123
IV.	Neoteinic Females.....	128
V.	Methods of Securing Males of the "Trilobite-larvae".....	131
VI.	Supposed Luminosity of the "Trilobite-larvae".....	132
VII.	The First Known Male and Female of the "Trilobite-larvae"....	133
VIII.	The Systematic Position of the Genus <i>Duliticola</i>	137
IX.	Food Habits of the "Trilobite-larvae".....	140
X.	Different Species of "Trilobite-larvae" from Borneo.....	142
XI.	"Trilobite-larvae" from other Parts of the Oriental Region.....	144
XII.	General Discussion of the Development of Lampyridae, Drilidae, Telephoridae and Lycidae.....	145
XIII.	Bibliography.....	151

I. INTRODUCTION

Among the many remarkable forms of insect life to be met with in the Oriental region none have aroused the interest of entomologists more than certain strange looking uncouth creatures, showing a great resemblance to the extinct trilobites in possessing protruding lateral processes on the abdominal segments. From time to time various "trilobite-larvae" as they have been termed by English entomologists, have been figured and more or less superficially described. Although the first one was made known in 1831 by Perty no one has been able to breed them and state what they really are. They have been a standing

¹Contributions from the Entomological Laboratory, of the Bussey Institution, Harvard University, No. 249.

puzzle to entomologists and for nearly a hundred years their systematic position, method of propagation, food, etc., have remained a mystery.

II. HISTORICAL

In the year 1831 Perty described a peculiar beetle-larva which he called "*Larva singularis*" or "*Larva quædam et Java*." He seemed to be inclined to regard it as the larva of a necrophagous rather than of a malacoderm insect and adds: "*Vi determinandum est cujus imaginis hæc larva sit.*"

In his "Introduction to the classification of Insects" (1839) Westwood mentions the same larva and refers it preliminarily to the Lycids. Furthermore he describes and figures a smaller larva with more nearly parallel-sided body, which he also considers to be a Lycid larva.

Some years later (1841) Erichson refers to a similar larva and believes it to be a Lampyrid. This opinion was shared 20 years later on (1861) by Candèze.

In 1887 or some 26 years later Kolbe discusses the "trilobite-larvæ" and inclines to Westwood's opinion that they are Lycids.

A larva referred to in 1887 by Lucas with "mandibules grands, arquée robustes" and with "plaques lumineuses" from Siam is apparently a Lampyrid-larva of some kind.

In 1899 Bolivar describes and figures two "trilobite-larvæ" of the broader type, one from Borneo and another one from the Philippines under the title "Dos formas larvarias de lampirides." Concerning their systematic position he seems to be in doubt. A figure of one was sent by Bolivar to Bourgeois, who in reply makes the following statements: "Quant à cette de Philippines elle est tout autre et je ne serais pas étonné qu'elle n'appartient pas au genre *Lycus*. Quoi qu'il en soit, cette larve de Philippines est de plus intéressante et il serait fort à souhaiter que nous puissions être édifiés bientôt sur les métamorphoses à quelle espèce nous devons la rapporter."

An examination of Bolivar's figures makes it clear that both larvæ are of the "trilobite" type. The one from Borneo is obviously the most common lowland form, which has repeatedly been figured or described by various authors.

The same year (1899) Dr. Sharp describes and figures a peculiar larva from New Britain in the following words: "There have long been known to entomologists some extremely remarkable larvæ, that probably are Lampyrides or Lycides, though none of them have been satisfactorily identified. Dr. Willey procured a most remarkable form of this kind, bearing long abdominal processes that are segmented or articulated at the base (Pl. XXXV, Fig. 7). "I take the opportunity", he adds, "of drawing attention to these forms with the hope that someone may soon be able to give us further information about them."

There can be hardly any doubt that the larva referred to is a Lampyrid larva, though of a very aberrant and extraordinary type.

In an article in the Sarawak Museum Journal (No. 3, 1913, pp. 61-65) Mr. Gahan deals in detail with the mysterious "trilobite-larvæ" and discusses the future possibilities of solving the problem which they present. He recommends strongly that tropical entomologists attack the problem in the field and make renewed attempts to rear them, pointing out, however, that larvæ have been kept alive a long time, extending up to two years, but so far without success.

The late Curator of the Sarawak Museum, Dr. R. Shelford, in his posthumous work "A Naturalist in Borneo" edited by Prof. Poulton, has dealt at length with the "trilobite-larvæ." He devotes several pages to these mysterious creatures, from which I extract the following:

Page 172: "If, then the adult male of the 'trilobite-larvæ' is provided with wings and wing cases, then the larva should possess imaginal rudiments, but a careful microscopical examination of male larvæ ranging from a comparatively small size to nearly the largest has failed to reveal the slightest trace of these organs. I can therefore declare with some degree of confidence that if an adult male of this larva be eventually found differing in its external anatomy from the larva, then it must be apterous. In spite of the abundance of these larvæ, in spite of the fact that they have been known to collectors for many years, a male of this description has never been found. I will venture to prophesy, moreover, that it never will be found, but

that some day a larva with completely developed internal generative organs communicating with the exterior by ducts will be found and such a "larva" will be to all intents and purposes an adult. If this is ever established, we shall have a gradual transition from species exhibiting complete metamorphoses to species without any metamorphoses at all as thus:

Males and females undergoing complete metamorphoses.

Lycidæ etc.

Males and females undergoing complete metamorphoses but female larviform. *Lampyris noctiluca*.

Males undergoing complete metamorphoses; females not metamorphosing. *Phengodes*

Males and females undergoing no metamorphoses, both indistinguishable from larvæ. "Trilobite-larvæ".

What Shelford means by "having examined male-larvæ ranging from comparatively small size to nearly the largest is certainly very difficult to explain. Obviously he presumes that some of the "trilobite-larvæ" commonly met with in the nature must be male-larvæ and therefore all his conclusions based upon this wrong supposition are wrong. For all "trilobite-larvæ" reared by me—and they number more than 50 and belong to three different species—have turned into females and we can therefore safely conclude that all the common "trilobite-larvæ" we find crawling about in the jungle are female-larvæ.

What furthermore seems to have puzzled Shelford is the extraordinary size of the larvæ. He states that "neither in Kina Balu nor in the neighborhood of Kuching, where 'trilobite-larvæ' also occur does there exist, so far as known a Malacoderm beetle that could possibly be regarded as the adult in either of these families and this in spite of the fact that in the one place the larvæ are extraordinarily abundant and in the other common enough."

It deserves furthermore to be pointed out that Shelford's above quoted statement about *Phengodes* is misleading. As we shall see later on, the members of the peculiar American group *Phengodini* pass through a long pupal stage and the larviform

female shows certain distinctive features in comparison with the larva.

The latest author to deal with the "trilobite-larvæ" is Gravely in his paper "The Larvæ and Pupæ of some Beetles from Cochin" (Records of the Indian Museum, Vol. XI, part V, No. 20, 1925). He describes and figures the larva of *Lyropæus biguttatus*, which in general type resembles the "trilobite-larvæ" although it is considerably smaller in size. The larva developed normally into a pupa and imago. Gravely states that "the larvæ which give rise to these winged insects are, however, not particularly large and throw no certain light on the status of the much larger insects with which the name "trilobite-larvæ is more particularly associated."

Gravely also refers to two large insects of the "trilobite-type" which were found in the Cochin forests. They are figured on plate XX and measure about 28 mm. He also mentions another larva of much smaller size also from Cochin, which has more elaborate tubercles and papillæ and differently constructed mouthparts. He suggests that these former larvæ may prove to be immature females of the Lycid genus *Lyropæus*, but leaves the question open as nobody has been able to trace their life-history.

III. NEW INVESTIGATIONS.

On arriving in Borneo in May 1922 I made up my mind to have the problem of the "trilobite-larvæ" of Borneo definitely solved more especially as my interest for these peculiar forms of life had been already aroused during my sojourn in Sumatra in 1919-21, when I came across a single representative of "Perty's larva" in the jungles of Siantar.

It has long been known that these peculiar larvæ reach their maximum of size in Borneo. So far as I have been able to ascertain at present two distinct types have been recorded from there and superficially described. To this I am glad to add four more, making a total of six species. One of them is a very striking form, measuring nearly 70 cm., quite black with a serie of sealing-wax red tubercles on the dorsal side. It is figure

on Plate III fig. 1 and is the largest and most conspicuous form known so far.

Since 1922 I had a large number of the larvæ under close observation and have made every effort to rear them. The first species that came in my way was the large attractive larva just referred to above. It was found quite commonly on the higher slopes of the unknown Mt. Murad, a high mountain situated in the North of Sarawak not very far from the Dutch boundary. Over 200 specimens in different stages were secured and kept alive in suitable cages, but none of them underwent any metamorphoses. Most of them were brought along six weeks later on when I returned from Mt. Murad on my way back to the Baram Station on the lower Baram River. Owing to the awkward conditions of transportation where everything had to be carried on the natives' backs, many of the larvæ died.

The sudden change in temperature from the cold mountain regions down to the steaming hot lowland naturally aided in reducing the number.

In January 1923 I undertook an expedition to Mt. Dulit (4000-5000 ft.). The number of surviving larvæ, about 30, were taken along, but soon died. Out of more than 200 larvæ only a single one developed into an adult female, distinguished from the full-grown larva only by possessing a sexual opening in front of the anal disc, surrounded by two simple genital valves. It lived for some days but owing to some difficulties in casting the skin on the apical segments it soon shriveled, became discolored from a black secretion and died.

A dissection showed the ovaries full of small whitish eggs, convincing me that I had to do with a sexually mature, fully developed female for the first time.

When arriving at Mt. Dulit on the Tinjar River, a large tributary to the Baram River, I found to my great surprise that another "trilobite-larva" of large size and of apparently unknown type was fairly common on the higher slopes from 3500-4500 feet. It is the big black larva of the type shown in Plate III fig. 2.

On returning to my headquarters in Kuching in March I brought more than a dozen very large larvæ with me. These were fed on decaying jungle wood, which was changed daily.

After some weeks of captivity one of the larvæ rolled itself up and was lying on the surface as though dead for several days. One morning I found that it had cast the larval skin and appeared quite whitish. It remained in that position for another five days whereupon the color changed into a dull yellowish-white. It soon started to crawl slowly about. A close examination revealed the interesting fact that it had developed a sexual opening on the eighth sternite surrounded by two small valves immediately in front of the anal suction disc.

Some days later on it started to lay eggs. These were small, whitish, perfectly round, measuring about one millimeter in diameter. They were deposited in small groups here and there or simply dropped wherever the female was crawling, sometimes as many as 15-20 at the same place. Egg-laying went on for about two weeks until over 300 eggs had been deposited. Every morning, when opening the door to the cage I found the female turning the top of the abdomen upwards in order to expose the sexual opening from which a clear drop of liquid was secreted.

Three more larvæ cast skins after a similar period of rest and turned into sexually mature females behaving in exactly the same way as the first one described above. They all died after having deposited from 300-400 eggs. Some months later more females developed, but no signs of any males could be seen.

In October I undertook a new expedition to Mt. Poi in Southern Sarawak. There I came across the very same big black larva just referred to. They were found at an altitude ranging from 3000-5000 feet and were quite numerous. Several developed into females and were exposed at suitable places in the jungle in hopes of attracting the males, but without success. The females were tied up with a string long enough to allow them to move about in a circle and were protected by a cage of wire netting with meshes more than an inch wide. Thus the males could easily gain access to the cages and the females were comparatively free but at the same time well protected.

All efforts were, however, in vain. I had to return again to my headquarters. During the following month (December) my native collectors brought me more than 200 big larvæ of the same type from another mountain, Batu Gadin, in the Lundu district,

where they had been despatched exclusively for the purpose of collecting "trilobite-larvæ." Of these more than 20 developed into adult females in quite the same way as the ones previously referred to. As no signs of males could be detected it became now more clear to me that the "trilobite-larvæ" commonly met with in the various localities must all be female larvæ.

In January 1924 I set out for a third expedition, this time to the second highest mountain in South Sarawak, Mt. Penrissen (4000 feet). The main object was to follow up the search for the males of the mysterious larvæ, all the available female material was brought along in two big cages. My supposition that the same type of larvæ probably would be found also on Penrissen turned out to be quite correct, for several larvæ of the same or at least very similar kind though not quite so big were found in close vicinity of my camp.

A number of newly developed females were immediately exposed in the same way as described before. As many as 18 cages were kept going. They were carefully examined three times a day, the first time always at sunrise. But although over a month was spent on the big mountain, covered with a luxuriant jungle, no traces of any males could be found.

It deserves to be mentioned that all "trilobite-larvæ" found on Mt. Penrissen were only half grown and showed more pronounced light markings between the dorsal rows of tubercles than the form from Mt. Dulit, Mt. Poi and Mt. Batu Gadin. It is therefore possible that it might have represented another species or sub-species and that both these facts may have been reasons why I did not meet with any success in capturing the males.

I returned to Kuching, determined not to give up my efforts to secure the males. As all the larvæ of the developed females had been collected on Batu Gadin, this place could be regarded as their true home and I therefore decided to move my base of operations there. In April 1924 I proceeded to Lundu and from there directly to Batu Gadin where my headquarters were erected at an altitude of 2500 feet.

During two weeks I supervised the experiments myself. Females of the ordinary types as well as of the smaller more

parallel-bodied kind which I had also been successful in breeding, were exposed at selected places but all in vain. As other duties called me to Kuching I had to return leaving my collectors behind with instructions to report immediately if any males should appear in the cages.

During more than two months this tedious work was kept going without the slightest results. In the meantime I visited the place twice making some slight alterations. The native collectors lost all hope, complained about the cold weather and wanted a change.

I gave, however, orders to move the experimental base 1000 feet higher up, where big larvæ seemed to be more plentiful, as the attempt to get the males had to be continued. A reward of \$10.00 for the first male stimulated the collectors very much in their efforts.

I returned again to Kuching but heard nothing from my collectors during the following weeks. I visited the place again and made several alterations placing the cages in more open places, exposed to the weather and wind, here and there clearing patches of the dense jungle vegetation.

This proved ultimately to be successful for one morning a male was caught in copula with a female. (Plate IV fig. 1). I was just on my way back, when one of my collectors came running after me with the copulating pair wrapped up in a banana leaf. At the ventral side of the big female a small black beetle was seen firmly attached and with his tip of the abdomen deeply inserted in the female's sexual opening.

It soon detached itself from the female and was preserved in alcohol. The female was brought back to Kuching where it soon started to deposit a large number of eggs, but unfortunately they never hatched out. Probably the male had been too much disturbed and the eggs had not been properly fertilized.

My collectors received strict orders to carry on the experiments in order to secure as many males as possible and to watch carefully the eggs deposited by the females. Four more weeks' work yielded a dozen more males of exactly the same type as the first one. It was therefore evident that I had, after **all my** trouble and effort, secured the proper **male**.

All deposited eggs were brought down to Kuching by the returning collectors, but for some unaccountable reason, not a single one hatched. Evidently the sudden change in altitude and temperature between the cold mountains and the hot lowland must be responsible for their failure to hatch.

As already stated females of the smaller and more narrow type of "trilobite-larva" had also been exposed, but no males were ever found. The females deposited about 100 eggs each. In spite of the female of this type being much smaller than the first one its eggs, as seen on Plate IV fig 2, are curiously enough twice as large.

Thus nearly two years of more or less continuous field work had resulted in rearing three species of "trilobite-larvæ" to egg-producing adult females and in the capturing of several males of the second largest species.

All my attempts to rear the very common, flat, leaf-like lowland species figured in Plate III Fig. 5, had been a failure. Although the larvæ were kept by me in hundreds in cages not a single one turned into a female. When attaining their maximum of size they were all attacked by a whitish mould which killed them in great numbers.

The only way to rear this species seems to be to build big cages in the forest and to keep some hundred of the largest ones in captivity under conditions as natural as possible until the females develop like the other species. The larvæ feed on decaying old wood. This type of larva is extremely abundant and it would be more interesting to get its male which, for reasons given below, probably represents a new genus.

IV. NEOTEINIC FEMALES.

A closer examination of the "trilobite-larvæ" from Borneo thus reveals the interesting fact, that the "trilobite-larvæ" so commonly met with are the female-larvæ of Lycid beetles of various genera and that the females undergo, practically speaking, no metamorphoses at all. They attain sexual maturity as complete larvæ and differ in their organization only by possessing developed ovaries and a sexual duct and opening. They are

adults retaining infantile characters and can therefore be termed neoteinic in the definition of GIARD (1905). The males on the other hand are well developed beetles probably hitherto undescribed but in all essential characters normally developed Lycids.

The female has so completely reduced her metamorphoses that in her external features, she is perfectly larviform. No marked pupa or imago-stage exists. As a worm-like creature she crawls sluggishly about on the ground and dies after having deposited her numerous eggs. Copulation and oviposition take place in a quite normal way. The female has specialized in the direction of larger size, premature development of the sexual organs and in reducing the normal metamorphoses to an absolute minimum.

It seems certainly strange that the female after the last ecdysis remains whitish and unpigmented. A close examination, however, shows that a diffuse casting of skin takes place after the development of the sexual organs, or in most cases after oviposition, when the body shrinks together and therefore the thin transparent skin becomes more conspicuous. (Plate III Fig. 2a). This partial casting of the skin seems to be more or less confined to the dorsal side and is probably the last reminiscence of a former regular pupal stage, which we must suppose the female to have possessed during earlier geological periods when it was more similar to the male and not yet so highly differentiated in the way of retrograde development.

It deserves in this connection to be mentioned that many, if not all of the normally developed Lycids show a distinct tendency to retain the last larval skin when pupating. When in Borneo I bred hundreds of the gregarious larvæ of *Lycostomus gestroi* Bourg. They all kept their skin when pupating. The advantages of this are apparent. The larvæ are black with bright yellow markings, which serve as warning colors. Their principal enemies, birds, reptiles and carnivorous insects know by experience their nauseous properties and a *Lycostomus* larva is therefore never attacked. The insect makes use of the well-known warning coloration to protect the whitish-yellowish pupa, by keeping the larval skin as a cover. The larval skin

bursts on the sides and the dorsal as well as the ventral sides remain covered by the brightly colored larval skin.

It is therefore possible that the diffuse casting of a thin skin in the female of the "trilobite-larvæ" after the oviposition or after the development of the sexual organs is to be explained as a reminiscence of the habits of its ancestors to pupate within the larval skin.

Strictly speaking the present day female of the "trilobite-larvæ" represents nothing more than a strongly condensed form of a larva and pupa and imago of a Lycid-female.

The larva is clearly indicated by the larva-like organization in general, simple eyes and mouth parts, one clawed-tarsi and 9 abdominal segments; the pupa by the general lack of pigment and probably by the diffuse casting of a thin postlarval skin; the imago finally by its sexual maturity.

The discovery of egg-laying larva-like females and the first male of the "trilobite-larvæ" of large size from Borneo makes it highly probable also that the other large "trilobite-larvæ" from Borneo and other parts of the Oriental Region are nothing but female-larvæ of Lycid beetles. When the male of the second largest species from Borneo has proved to be such a small Lycid it is probable that the males of the other smaller species belong to the smaller forms of the Lycidæ. The characters of the first male known point decidedly towards a fairly close relationship with the genus *Dihammatus* of which so far as I am aware only three species are recorded from Borneo (*D. pallens*, *D. abditus*, *D. bornéensis*), some few other ones from Java, (*D. cribripennis*) Sumatra, (*D. atriceps*) and Formosa (*D. atricolor*).

That our knowledge of the Lycid beetles is, indeed, only in its infancy is clearly shown by the large number of new genera and species described by the well-known German entomologist, the indefatigable Mr. R. Kleine. My own material from my expedition to the unknown Mt. Murad has already been worked by Mr. Kleine and his results will be published in the next number of the Sarawak Museum Journal. More than 66% of the forms are unknown and there are many new genera. Professor C. F. Baker of Manila, who so keenly and in a most admirable way

has devoted his time and efforts to the exploration of the insect-fauna of the Philippines, informs me that Kleine recently has doubled the number of Philippine Lycids.

Unfortunately I was not able to study the development of the eggs which may prove to be of extraordinary interest. When the male and the female are so extremely different not only in size but in their whole organization, it is highly probable that the male-larva is very different from that of the female, *i. e.*, the "trilobite-larva" we find crawling on the ground. Are the male larvæ already "*ab ovo*" different to the female-larvæ and of what shape and form are they? And how large a percentage of a female's 300-400 eggs turn into males, how many into females? Where and how do the male-larvæ live and where the males, both being obviously extremely hard to find?

All these interesting questions remain to be settled!

METHODS OF SECURING MALES OF THE "TRILOBITE-LARVÆ."

It is certainly strange that the "trilobite-larvæ" have for so long frustrated the efforts of the entomologists to solve their mystery. I am quite sure that if I had not been so persistent in my searches and during so long a time devoted special attention to the problem in the field. I also should have failed.

My experience clearly shows that the males of the "trilobite-larvæ" can be got only by bringing together a large number of the larvæ and keeping them under conditions as natural as possible until they turn into egg-laying forms. These have to be exposed at suitable places where the larvæ are abundant and during the wet season, when the males seem to have developed into winged beetles. Change in temperature and altitude should be avoided so much as possible. Finally the hunter should arm himself with great patience!

Such exposure at the right place remains to be done with five more Bornean forms and with the various larvæ found in Java, Sumatra, Malay Peninsula, Cambodja, Indo-China and the Philippines, from which latter faunistic region Professor C. F. Baker with usual generosity and kindness has sent me a couple of species from the Island of Mindanao.

SUPPOSED LUMINOSITY OF THE "TRILOBITE-LARVÆ."

It has been stated from time to time that some of the "trilobite-larvæ" are luminous.

The first entomologist to make such a statement was Kolbe (Ent. Nachr., No. 3, 1887, page 38). He states that "Das Königl. Museum bekam wieder um eine Anzahl dieser Larven von Hr. von Faber, die derselbe in Padang an der Westküste von Sumatra gefunden hat und welche anscheinend übereinstimmen mit den schon seit langer Zeit in Besitz des Königl. Museums befindlichen Exemplare aus Java. Nach Angabe der dortigen Bewohner sollen sie im Dunkeln leuchten, aber ich habe keine Gelegenheit gehabt es selbst zu sehen. Man sieht daher dass nicht nur die Larven der Lampyriden und einiger Telephoriden (Phengodes) sondern auch von Lyciden leuchten."

As seen this statement is entirely based upon the natives' vague information. It is more than credible that a confusion with *Lampyrid* larvæ has taken place for no other reliable entomologist, who has handled "trilobite-larvæ"—with one exception, which will directly be dealt with—has been able to observe any luminosity. Kolbe's conclusion that certain Lycids show luminosity is certainly very rash and can hardly be taken seriously.

The only white observer who mentions something about personal experience with luminous "trilobite-larvæ" is Shelford (Rep. Brit. Assoc. 1901, page 690). In a short note he refers to: "Some other Malacoderm larvæ of considerable size (50-80 mm.) were frequently met with, but their life-histories were not traced; in fact these larvæ have long been a complete puzzle to entomologists, since no adults of corresponding size are known. The external features of one form has recently been described by Bourgeois (Bull. Soc. Ent. Fr. 1899 page 58-63); the head is extremely like that of the Lycid larvæ noted above and in other points of its anatomy it agrees with those forms. In another form with a pair of phosphorescent organs in the penultimate segment of the abdomen the cuticle is glandular."

To what larva the latter statement refers, we get no further information. I have carefully examined all the "trilobite-larvæ" in the Sarawak Museum, but fail to find even the slightest trace

of luminous spots or organs in any of them. The very same thing applies to all the various "trilobite-larvæ" I have handled in a living state.

As it is hardly credible that Shelford had access to any other "trilobite-larvæ" than those that I have seen, I think we can safely conclude that he has based his statement on a Lampyrid larva, many of which occur in Borneo, some reaching a fair size.

I therefore maintain that so far no definite and convincing statement about luminous Lycids exists.

THE FIRST KNOWN MALE AND FEMALE OF THE
"TRILOBITE-LARVÆ."

Duliticola gen. nov.

♂: Somewhat allied to the genus *Dihammatus* but differing by having more strongly developed and more curved mandibles, the 2nd and 3rd joint of antennæ more sharply set off from the

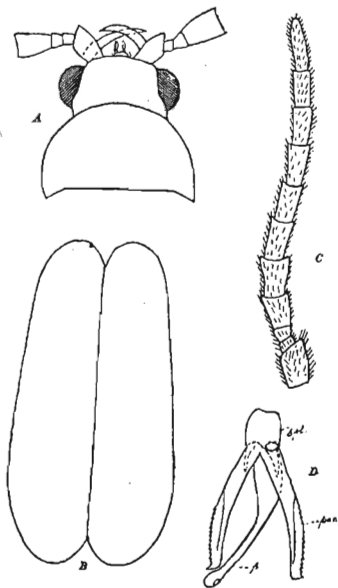


Fig. 1. Male of *Duliticola paradoxa* op. nov. A, head and prothorax from above; B, outline of elytra; C, antenna; D, genitalia.

others, the joints more transverse, slightly emarginate at the dorsal end, laterally more compressed and more strongly hairy; prothorax more semicircular with the sides more plainly set off and more rounded, stronger and more robust; legs and the genital apparatus in the male of much more slender and much different type.

Head broad, transverse; antennæ distant, long and slender, second and third joints much shorter than the others; eyes large, prominent, coarsely faceted. Prothorax semicircular, lateral parts flattened and plainly set off by a deep impression. Elytra showing signs of indistinct ribs, interstices slightly rugose, increasing considerably in width backwards, richly hairy; wings of the ordinary Lycid-type, but membrane strongly infusate giving the whole wing a blackish appearance. Legs richly hairy; tarsi long and slender. Abdomen showing eight transverse segments, all finely hairy, the eighth tergite at the anterior margin deeply excised; genital segment consisting of a dorsal elongate lamella and a much shorter ventral one; penis and paramera of a slender type as shown in text fig 1, D; paramera hooked at the apex, distinctly serrated at the lower margin, apparently forming an effective clasping-apparatus during copulation.

♀: In everything like the female larva (*vide* description below) but yellowish white; the row of tubercles on the sternites placed on more distinctly set off parts of the segments; the eighth sternite very much emarginated at the hind margin and here the sexual duct, surrounded by genital valves, opens (Plate III fig. 2a).

Size slightly smaller than in the full grown larva, ranging from 65-75 min.

Duliticola paradoxa sp. nov.

Imago.

♂: Entire body with the exception of the somewhat lighter colored sides of prothorax black, depressed, broader behind.

Antennæ long, laterally compressed, densely hairy, basal joint robust, partly receiving the base of the second, which is

short and cylindrical; third much broader than long, tapering toward the base, fourth to sixth about one and one-half times longer than broad; slightly emarginate at the apex, seventh to tenth gradually becoming longer and more slender, apical joint the longest, being fully four times longer than broad, at the apex rounded. Frons vertical, labrum thin, membranaceous, tapering anteriorly, slightly emarginate in front and here transparent; mandibles very strongly developed, perhaps serving some purpose in copulation, maxillæ and labium of the normal type; sides of head behind the eyes strongly converging backwards. Prothorax more than twice broader than long, nearly semicircular, disc with a slight transverse basal impression, shining, hind margin emarginate, hind angles slightly protruding, obtuse; scutellum fairly big, triangular, rounded at the tip. Elytra showing a tendency to develop faint longitudinal costæ, widened towards the tips, posteriorly rounded; tibiæ long and slender; claws with a small tooth-like dilatation at the base. Abdomen narrow, the first seven segments fairly equal in size, hairy. Measurements: Total length 7 mm. greatest width 2.7 mm.

Habits: Nocturnal.

Locality: Mt. Batu Gading near Lundu, altitude 1500-3000 feet, Sarawak. Probably distributed over a wide area. Its ♀ larvæ found by me (1 spec.) near Lio Matu on the Baram River and on Mt. Dulit on the Tinjar River, North Sarawak, altitude 2000-4000 feet.

♀ (Plate III fig. 2a): Of very large size, in general shape and appearance like the female-larva, but yellowish-white.

Measurements: Slightly smaller than the full grown larva, ranging from 65-75 min.

ADULT-LARVA

♀: Body black, except a small median patch at the posterior margin of all thoracic and the first eight tergites, which is yellowish; abdominal processes and lateral margin of thoracic segments whitish; the whole upper surface finely shagreened and punctured. Head small, completely retractile within the prothorax; antennæ retractile, two-jointed, terminal joint hairy,

provided with several holes in the chitin where probably sense organs of some kind are placed; mouthparts very incompletely developed, mandibles curved, more or less membranaceous and folded horizontally, maxillæ small, maxillary palpi three-jointed the second joint only half the size of the basal one, the apical joint very small, weakly pointed. Labium anteriorly forming a small chitinous ring on which the small 2 jointed labial palpi are inserted, the terminal joint pointed; head forming a solid chitinous case, sides from the base of the antennæ to the small simple eyes parallel, from these converging backwards; eyes in the living animal marked by a small pigmented spot. Prothorax forming a large triangular shield, in the middle of the front margin with two small tubercles and two corresponding ones on the ventral side, hind angles obtuse, at the posterior margin in the middle with two small black shining tubercles; meso- and metathorax broader, more rounded at the sides, both with a pair of small black tubercles separated by a yellowish patch at the hind margin, both segments with a pair of extraordinary large spiracles. Legs consisting of a long and robust coxal part, a trochanter-like one, a tibial and a tarsal one which is hairy below and bears at the end a single strong and sharp claw. Abdominal tergites nine in number, the first seven fairly equal in size, the eighth and ninth gradually becoming smaller, the hind angles of all segments protruding as a backwardly bent process of lighter color and with a pair of black tubercles separated by a yellow patch, except on the apical segment, where the tubercles are missing; posterior margin of last segment slightly sinuate; the corresponding sternites show the lateral parts set off by a deep furrow, in the middle with two rows of protruding spines, which at the top carry a tuft of dirty white bristles. On the distinctly set off lateral portions of the segments there are two rows of tubercles, one interior consisting of small black tubercles and one exterior row of large slightly curved processes which become lighter colored towards the tips; obviously these rows of ventral tubercles serve for locomotory purposes, enabling the larva to move about on the loose jungle soil; the terminal segment with a large circular round whitish suction disc.

Measurements: Total length 75-80 mm. Greatest width of metathorax 25-30 mm.

THE SYSTEMATIC POSITION OF THE GENUS *DULITICOLA*.

From what has been said above the genus *Duliticola* possesses all the essential characters of the family Lycidæ and should therefore be placed there.

When still in Borneo I tried hard to identify the first known male of the well-known "*trilobite-larvæ*". Owing to lack of access to literature I could not settle the question locally. I therefore sent a specimen to the well-known entomologist Mr. C. F. Gahan of the British Museum asking him for his opinion. Mr. Gahan informed me that he considered the beetle to be a Lycid and belonging to a genus related to or perhaps identical with *Dihammatus*.

Later on I sent also a specimen to the well-known German entomologist and Lycid specialist, Mr. R. Kleine of Stettin, who declared that no Lycid of any similar type was known to him and that he thought the beetle to be a Drilid.

Before leaving Borneo I was kindly offered an opportunity by Professor W. M. Wheeler to come to America and to take up some research work at the Bussey Institution. I gladly accepted his invitation and had there an excellent opportunity to go into the question in detail myself.

There can in my mind hardly be any doubt that Gahan's statement that the beetle is a Lycid is correct. My close examination, however, shows that it can under no circumstances be placed in the genus *Dihammatus*. It differs distinctly in the shape and build of the antennæ, the shape of the prothorax and above all in the male genital apparatus, from a specimen of *Dihammatus abditus* Kleine which Mr. Kleine has been kind enough to send me for comparison.

The reasons why Kleine seems to favor a position in the Drilidæ are partly because the middle-coxæ of my beetle are not quite so distant as in most Lycids, and partly because normally developed females of all known Lycid-genera are known.

With reference to Kleine's first objection, I find that the characters "*coxæ contiguous*" and "*coxæ distant*" are fairly

relative ones, different degrees of both being traceable within the family Lycidæ. The male-specimen of *Dihammatus abitus* Kleine from Sandakan in North Borneo, treated with caustic potash shows the middle-coxæ more nearly contiguous (less distant) than in the males of *Duliticola paradoxa* Mjög, treated in the same way. I therefore consider that not too great stress should be laid upon this character.

It is certainly a strange fact that not a single of the many known Lycid-genera known up to now are characterized by larviform females, normally developed females of all described genera according to Kleine being known.

As I find that my beetle can not be received in any of the known genera I have been forced to create a new one. The fact that no similar beetle is represented in the rich collections of the Sarawak Museum and in no other collections I have seen (Singapore, Java, Manila) would certainly point to the belief that the male of *Duliticola paradoxa* Mjög. as well as of the other "trilobite-larvæ" must be extremely hard to get. It took me fully two years of more or less continuous field work to procure the first male and it was only thanks to the numbers of sexually mature females exposed and to my persistent attempts that I was successful in securing it. Obviously the males must live in such a hidden way that they do not fall in the hands of the chiefly diurnal entomologists and collectors. The circumstances that they are exclusively nocturnal and non-luminous have also much weight. Also the fact that the males are not attracted by strong light helps to explain why they have so far escaped all entomologists. During my long and tedious nights in the Bornean jungle I kept permanently two big light traps going, consisting of a big basin in four sections filled with water and measuring about a meter in diameter with a 250-candle power lamp ("Storm King") hanging immediately above the water. Every night thousands of smaller creatures were attracted and caught on the water. Among the victims were several male lampyrids of the genera *Lamprophorus*, *Lucernuta*, and *Luciola* but not a single male of *Duliticola paradoxa* Mjög.

As all observed males of *Duliticola* seem to die directly after the copulation it is probable that they fertilize only one

female. That they are not so scarce at the right place and at the right time is evidenced by the fact that my collectors managed to catch over a dozen specimens at the very same place, after I had found out the right way to expose the females.

As full grown female-larvæ can be collected in great numbers, sometimes in hundreds within a shorter time than a week, and at almost any time of the year, it is only logical to conclude that males also must be developed fairly regularly, since parthenogenesis does not seem to occur. That there is no standstill in the tropics is a well-known fact and it is indeed corroborated by the fact that larvæ kept in captivity by me continuously developed into mature females the whole year round.

It seems therefore probable that the males, guided by their senses, find their way directly to the hidden females and die on the spot immediately after copulation. This may be the explanation why they are so rare in nature and have so far escaped entomologists and collectors. The same obviously applies to the females which can be said to be still more scarce, as in no single instance has a mature female yet been found in the field. The life history of the imagines of both sexes is therefore still wrapped in mystery.

The type of antennæ and the general structure do not permit me to place the genus *Duliticola* within the family *Drilidæ*, all known females of which are carnivorous. This applies also to the *Drilid* larvæ known up to now, which are very different from the "*trilobite larvæ*" in all more important features, while these latter undoubtedly remind one strongly of certain *Lycid* larvæ, for instance, the larva of the genus *Lyropæus* as described by Gravely.

It is, however, a noteworthy fact that *Duliticola* and in all probability also the other genera of "*trilobite-larvæ*" which undoubtedly soon will be discovered, differ strongly from the ordinary *Lycids* in following striking features:

1. Neoteinic larviform females.
2. No externally visible metamorphoses in the female sex.
3. Female larvæ reaching a gigantic size, with reduced mouthparts.

4. Non-carnivorous, non-gregarious, feeding on decaying damp wood.

As pointed out previously the "trilobite-larvæ" must belong to different genera. As normally developed females are known of all described Lycid genera and as it is utterly incredible that one and the same species should possess both winged and larviform females normally as Gravely suggests (*l. c.* p. 362) I venture to prophesy that several new genera of "trilobite-larvæ" will be described in the future. If these should possess more strange characters than does *Duliticola*, compared with normal Lycids (*viz.*, *Dihammatus*) it would perhaps be justifiable to separate the group of "trilobite-larvæ", characterized by so many strange features and habits, as an offshot of primitive Lycoid beetles and give them the rank of a family or sub-family of their own (*Duliticolidæ* or *Duliticolinæ*) related to the other four groups of malacodermata and *via* *Duliticola* more so to the Lycids than to the Lampyrids and Drilids.

But at the present moment our knowledge of these queer creatures is too scanty to justify such a step.

FOOD AND HABITS OF THE "TRIBOLITE-LARVÆ."

The "trilobite-larvæ" are chiefly found on or in the vicinity of big rotten logs, sometimes several near the same spot, but as a rule they do not show any tendency of being gregarious, odd larvæ often being found crawling about anywhere in the jungle. They like rainy weather and are mostly found crawling around after heavy showers.

The larvæ feed on the juice of decaying wood, as clearly evidenced not only by the contents of the stomach but also by direct observations. But they seem to be very particular in getting the right kind of wood. When changing food every day I had many opportunities to study their behavior. Often they crawled over the new pieces of wood put in the cage until they came to the proper kind. There they used to accumulate and I could plainly see by aid of a powerful magnifying glass that they actually were sucking the juice from the wet pieces of wood. Larvæ killed and examined some hours afterwards were found to

have the stomach and intestines full of a dark mass of decayed woody products, reminding one of the material found in longicorn larvæ.

When touched the larva withdraws its head very quickly and remains still for a time. Slowly the head is again thrust out and the larva continues its slow crawling.

When taken between the fingers the larvæ secrete a kind of milky white substance between the segments and the joints of the legs, which apparently serves some protective purpose. No living being in the jungles seems to be inclined to attack or feed upon the larvæ on account of their nauseating properties. In the numerous stomachs of birds which I purposely examined in search of parasites, I have failed to discover any remains of "trilobite-larvæ."

Peculiarly enough I have never been able to find larvæ of smaller size than 15 mm. Probably the female deposits her eggs in the interior of big hollow decaying logs and the young larvæ remain in their birth place until they have cast the skin several times.

The larvæ grow very slowly, as many of them kept by me in captivity have remained unchanged and cast no skins during more than six months. In all probability the larva requires several years to become full grown.

It is equally strange that one never finds the adult females in nature. Although having for years hunted through the jungles in search of other invertebrates, both myself and my trained collectors, and having turned every stone and split up thousands of pieces of decaying wood or heavy logs I have never been able to find a single fully developed female, in spite of the fact that full grown larvæ were abundantly common thereabouts. Where she undergoes her last ecdysis still remains a mystery. As the larvæ are very feeble, helpless creatures they can neither live a subterranean life by digging themselves down into the ground nor by boring themselves into the wood. It is, however, possible that the female manages to reach the interior hollow parts of a big heavy log, which is comparatively sound and where entomologists do not gain access.

DIFFERENT SPECIES OF "TRILOBITE-LARVÆ" FOUND IN BORNEO.

The following types of "trilobite-larvæ" are known to me from Borneo:

No. 1. (Plate III fig. 1)

♀ : *Larva*: A very large remarkable form, shining black with a row of four bright sealing-wax red tubercles at the hind margin of the thoracic segments and two rows of median sealing wax red tubercles on the hind margin of the first eight abdominal segments. Also the margins of the thoracic segments of the abdominal segments are of the same bright color. The anterior prothoracic margins show two small tubercles or processes just behind the head; the prothorax is of a triangular shape, with rounded, obtuse hind angles, the sides of the meso- and meta-thorax are more parallel; all three segments are distinctly punctured and with a slight median, smoother elevation.

Measurements: Greatest length 92 mm., greatest width 20 mm.

Locality: Mt. Murad, N. Sarawak.

Altitude 4000-7000 feet.

Adult ♀ : In everything similar to the above described larva, but with a sexual opening, surrounded by genital valves on the eighth sternite. Color yellowish-white. Size slightly smaller than the larva. ♂ unknown!

No. 2. (Plate III fig. 2)

♀ : *larva*: *Duliticola paradoxa* sp. nov. *vide* description above.

Adult ♀ : *vide* description above.

No. 3. (Plate III fig. 3)

Cinnamon colored, with two black shining tubercles on the thoracic and the first eight abdominal segments; the abdominal lateral processes dark colored. Prothorax more rounded behind than in larva No. 1 and the hind angles smaller, metathorax with more protruding hind angles.

Closely related to No. 1 and probably belonging to the same genus.

Measurements: Greatest length 80 min.

Greatest width 18 min.

Locality: Mt. Murad, N. Sarawak. Altitude 6500 feet.

Adult ♀ and ♂ unknown!

No. 4. (Plate III Fig. 4).

Resembling No. 3; cinnamon colored like it, but the posterior prothoracic angles more rounded and the meso- and meta-thorax differently shaped, the rows of tubercles not so pronounced and between them a dark colored fascia. Otherwise like No. 3 and probably a species of the same genus.

Measurements: Greatest length 45 min. (if full grown?)

Greatest width 16 min.

Locality: Mt. Dulit, N. Sarawak.

Altitude 3500-4000 feet.

Adult ♀ and ♂ unknown!

No. 5. (Plate III Fig. 5).

The ordinary common type from the lowland frequently mentioned and figured by various authors.

Body strongly depressed, thin as a leaf, light brown, thoracic segments strongly dilated, with a streak-like mark on each side.

Measurements: Greatest length 40 min.

Greatest width 25 min.

Locality: Kuching and surroundings, Ramboengan, Lundu, South Sarawak. Especially common during the rainy season (Nov.-March).

Adult ♀ and ♂ unknown!

Represents another distinct genus!

No. 6. (Plate III Fig. 6).

The type figured and briefly described by Westwood. Of much more elongate and parallel-sided type than the previous ones.

Measurements: Greatest length 50-55 min.

Greatest width 13 min.

Distribution: Kuching, Lundu, and some other lowland localities, South Sawawak.

Larva of very similar or identical type occurs also in the Malay Penninsular and Sumatra.

Represents a distinct genus!

♀ *Adult:* In everything similar to the ♀ larva and like it colored dark brown although a diffuse casting of the pupal skin seems to take place.

♀ :-Unknown!

The above mentioned larvæ represent, to judge from their external appearance, the following genera:

I. A probably unknown genus with No. 1, No. 3 and No. 4 as species. (All mountain-forms!)—Borneo.

II. A new genus related to *Dihammatus* and described above as *Duliticola*. The larva of the only known species represents a type of its own quite unlike the other ones.—Borneo.

III. A genus of its own and on account of the abundance of the larva probably of an already described genus, but which?—Borneo.

IV. A genus of its own, but not so far known. Quite a distinct type.—Malay Peninsula.

"TRILOBITE-LARVÆ" FROM OTHER PARTS OF THE ORIENTAL REGION.

From time to time there have been "trilobite larvæ" specifically described and figured from Java, Sumatra, Malay Peninsula, Cambodia, Cochin, Burma, Ceylon, the Philippines, etc. How many species and genera they really represent it is impossible to state with our present scanty knowledge.

I have personally seen only the larva No. 7 of Plate III which was sent me from the Kuala Lumpur Museum and which comes from the Malay Peninsula. It is somewhat similar to larva No. 5 from Sarawak, but has more strongly and differently developed tubercles on the thoracic segments, and is surely specifically, if not also generically distinct from the Bornean one. Its body is not so flattened and its size larger (45 mm.).

Of the Philippine larvæ I have seen a collection belonging

to the Bureau of Science, Manila, and think that there are at least three different fairly closely related types or species represented. They all come from the island of Mindanao. The only hope of solving the identity of the species would be to send a trained entomologist to the island with strict orders not to return before he has endeavored to breed them out.

GENERAL DISCUSSION OF THE DEVELOPMENT OF LAMPYRIDÆ,
DRILIDÆ, TELEPHORIDÆ AND LYCIDÆ.

Of these four families, forming the group of the Malacoderms (*s. str.*) the Lampyrids show a marked tendency to develop larviform females, the retrograde development being confined chiefly to the elytra and the wings. All degrees of reduction seem to be represented, from females exactly like the males with fully developed elytra and wings down to entirely apterous larviform females.

It is of interest to note that a reduction also seems to take place in some of the males. But all males have wings except in the genus *Phosphænus*, where the elytra are reduced to small rudimentary lobes, the wings entirely absent.

All Lampyrid-females pass through a normal pupal stage and the imagines are characterized by possessing well developed antennæ, compound eyes, two claws, etc. No traces of hyper-metamorphosis can be found.

In the family Drilidæ conditions are practically the same, though slightly more complicated. The larva in its first stage is quite different from the so called "inactive form" or second stage, which is more like the pupa and therefore has been termed "pseudopupa."

According to Grawshay (Trans. Ent. Soc. Lond. 1903., pp. 39-51.) "the winter form into which the undeveloped larva changes about the middle of September, or often earlier, as stated, is incapable of feeding or of more than a heavy grub-like motion, when disturbed. In general outlines it much resembles the ordinary form of larva but it rather perhaps deserves the term "false pupa." The setæ are absent, the body being almost entirely soft, of whitish color and except on the last three or

four segments, almost hairless. The head is small and pale with the mouth parts rudimentary and the antennæ very short, modified. The legs are soft and short with the claws absent and replaced by a small prominence. The processes of the body are much smaller and less distinct, with only a few white hairs, until the last three or four segments where they become rather thickly hairy, but with the hairs shorter than in the larva. The terminal processes are likewise shorter but with the spines long (Plate III. Fig. 2a). This skin is cast about the middle of May and the larva then reappears from the shell in its ordinary form continuing its life as before, until it is full fed in the second or probably in most cases the third summer. When full fed it changes into a second inactive winter-form which more nearly approaches the pupa and which like the other, may be aroused early or late in the year. Though this is very similar to the previous one, it differs from it especially in the much more stumpy form of the antennæ and of the processes of the last three or four segments."

Another author, Rüschkamp, (Biol. Centralbl., 1920, page 376-389) corroborates Grawshay's above quoted statements about the life history of *Drilus flavescens* and gives the interesting information that he has been able to shorten or prolong the different stages by changing the degree of humidity and food. Such change of a larva from an active to an inactive stage could be brought about after only thirteen days. The larva seems to have the ability of adapting itself to the prevailing circumstances by changing over from the active to the inactive stage, whenever necessary or "*necessitate coacta*," an extraordinary thing showing how plastic in their habits certain members of the large and undoubtedly primitive group of malacoderms are.

The pupa of the male Drilid is a normal beetle pupa. The female pupa resembles very closely the last inactive form of larva. Thus a tendency to reduce and simplify the originally normal pupal stage is clearly distinguishable.

The females of the few Drilids, the life history of which is known are even more larviform in their general appearance than are the Lampyrid females. A distinct resting period is undergone and the female is in all essential characters an imago,

possessing many-jointed (10-11) antennæ, compound eyes and two claws, but lacking all traces of elytra and wings and therefore extremely larviform.

It is in this connection of interest to note that in the female also a reduction of the antennæ is noticeable. These show only ten joints, the apical one being reduced to a small appendage only, reminding of the small accessory appendage often found in the larval antennæ.

In some cases even a further reduction seems to take place. According to Grawshay "the antennæ of the female are normally composed of 10 joints (omitting the supplement) but the ninth joint is often imperfectly formed being sometimes confounded with the preceding one so as to be scarcely visible, and sometimes entirely absent." This deformity may even appear in different degrees in the two antennæ of the same insect. The Drilids therefore show a much greater degree of retrograde development than the Lampyrids.

The extensive group of the Telephorids shows as a rule quite normal conditions. Both sexes are equally well developed and typically predaceous, in this latter respect agreeing with the larvæ of the two previously mentioned groups. A strikingly exceptional type, however, is the remarkable American group Phengodini, where the sexes differ greatly from each other.

Thanks to Haase's excellent paper (Zur Kenntnis von *Phengodes*, Deutch. Entom. Zeits. 1888) we know that the Phengodes female has developed in a retrograde direction to an extremely larva-like creature. The male on the other hand is an elaborately developed beetle with highly specialized antennæ. According to Haase and Riley the female differs from the larva only by having "more feeble mandibles and tarsi" than the larva. It passes, however, a distinct pupal stage as is also corroborated by Mr. H. S. Barber in a letter to me.

In Sharp's "Insects" of the "Cambridge Natural History" the following startling statement about Phengodes is found:

"There is no reason to doubt that Haase was correct in treating the insects we figure as a perfect insect; he is, indeed corroborated by Riley. The distinctions between the larva and female imago are that the latter has two claws on the feet instead

of one, a greater number of joints in the antennæ and less imperfect eyes."

The source of this error of Sharp's is difficult to find. As stated previously no such distinctions do exist as already pointed out by Haase and Riley and furthermore corroborated by Mr. Barber in a letter to me of recent date.

Through the kindness of Mr. Nathan Banks I have had the opportunity of examining two larvæ and a female of *Phengodes*. There can be no doubt about the error of Sharp's statement. No such differences as pointed out by him exist. But on the other hand the differences between the female and the larva seems to be great. Whereas the fully grown larva is a pale-looking soft-bodied creature with a comparatively small head, the adult female in general appearance more suggestive of an Elaterid-larva, shows strongly chitinized, dark brown tergites with large, yellow, more or less square patches indicating the site of the luminous spots. The head in general and the mandibles are much more strongly developed, as well as the legs. In many ways the female really conveys the impression of an imago. When preparing for pupation the *Phengodes* larva burrows itself down in the ground and rests for a period of several weeks.

Like the Lampyrid Drilid and Telephorid larva the *Phengodes*-larva is carnivorous, and according to observations feeds upon myriopoda of the family Julidæ, which are often subterranean in their habits.

The specialization *via* retrograde development in the *Phengodes* female is thus carried to an extreme, the female being more vermiform than in the three previously mentioned groups, but still showing certain distinctions from the larva and still undergoing a pupal stage.

Finally, in the fourth group, the Lycidæ, both males and females are normally developed beetle imagines. Their larvæ so far as known, are Lampyrid-like, carnivorous and in some cases at least gregarious.

The only genus showing a tendency to develop reduced females seems to be *Homalisus*, the systematic position of which, however, does not seem to be definitely settled. Thus according

to Fowler (The Coleoptera of the British Islands, p. 126) "the synthetic genus *Homalisus* ought perhaps to be removed from the family (Lycidæ) and regarded as is done by some authors as a separate family in itself."

In his splendid work, "Fauna germanica" Reitter keeps the position of the genus *Homalisus* in the Lycidæ and adds with reference to *H. frontes bellaquei* Geoffr: "Das sehr seltene ♀ hat nur ganz kurze klaffende Flügeldecken und die Tergiten liegen frei."

I have not been able to find any more recent references to the genus *Homalisus*. But in all other respects the female is a normally developed beetle.

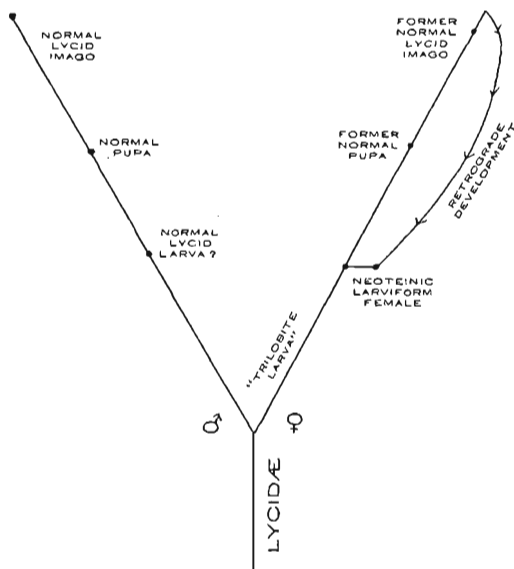


Fig. 2. Diagram illustrating the types of metamorphosis in the Lycidæ.

As a very striking example of retrograde development among the Lycid females we must now add the females of the Bornean "trilobite-larvæ". All the three vermiform females I have been successful in breeding (*Duliticola paradoxa* and the females marked as No. 1 and No. 6 (Plate III) show no differences whatsoever from the larvæ except in color and in

possessing sexual organs, ovaries, duct and aperture; and pass through no marked pupal state. The full grown larva simply rolls up openly for some days as does the larva when casting its skin, sheds the larval skin and turns into an adult female with the same head, simple eyes and one clawed tarsi as the larva. The two females bred without any complications (which as stated before happened to No. 1) behaved in exactly the same way, kept still for some days and started to deposit eggs and to expose the sexual opening by turning upwards the tip of the abdomen and secreting from the sexual aperture a drop of clear liquid.

The small group of Lycids which has developed in this queer direction, of which the larvæ up to now have been known as "trilobite-larvæ" is confined to the Oriental region. They belong undoubtedly to several genera and represent the most degraded forms known among the non-parasitic beetles. Judging from the abundance of the larvæ in the field, their peculiar regressive development seems to be a successful specialization. They differ also from normal Lycids by being non-carnivorous, with their mouthparts very much reduced, enabling them only to suck the juice of decaying wood. Their larvæ are further more non-gregarious and typical jungle insects, whereas most Lycids are gregarious and love sunny open places.

The group apparently reaches its maximum of size and variety in Borneo. Up to now six distinct forms are known from there, but future investigations will undoubtedly show that the "trilobite-larvæ" are richly represented in the central mountain chains of Borneo, a region which, however, still falls outside the beaten track.

It has long been established that the Malacoderms have to be placed among the more primitive forms of beetles. This explains partly why the members of this group which is in many ways undifferentiated display great plasticity in various directions. In all four families we find steps towards higher specialization mostly in retrograde direction, this applying chiefly to the females. In the Drilids a kind of hypermetamorphosis is found. Some of the Lampyrids show prothetely (*vide* Williams, *Psyche*, Vol. XXI. No. 4, pp. 126-129).

The most degraded forms are undoubtedly the females of the "trilobite-larvæ" which have reduced the metamorphosis to an absolute minimum and are practically larvæ with full possibility of propagation.

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EXPLANATION OF PLATES.

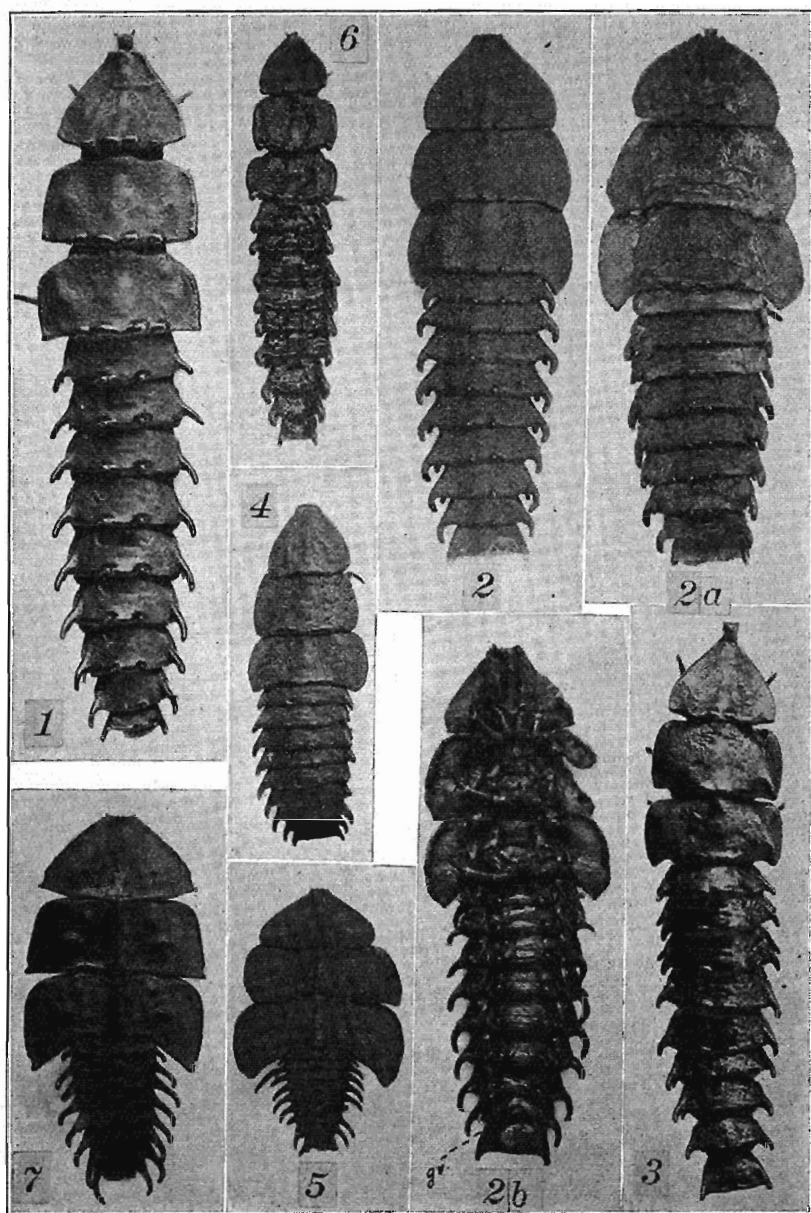
Plate III

1. "Trilobite larva" No. 1, Borneo.
2. Larva of female of *Duliticola paradoxa* gen. nov. and sp. nov.
- 2a. Adult female of *Duliticola paradoxa* gen. nov. and sp. nov.
- 2b. Ventral view of same.
3. "Trilobite larva" No. 3, Borneo.
4. "Trilobite larva" No. 4, Borneo.
5. "Trilobite larva" No. 5, Borneo.
6. "Trilobite larva" No. 6, Borneo.
7. "Trilobite larva" No. 7, Malay Peninsula.

Plate IV

Above: Male and female of *Duliticola paradoxa* gen. nov. and sp. nov. in copula *capta* (Twice natural size).

Below: Female of another species with eggs which she has deposited (natural size).



MJÖBERG—"TRILOBITE LARVAE"



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