VIII. *Notes on the Life History of* Gongylus gongyloides, *a Mantis of the Tribe Empusides and a Floral Simulator.* By Captain Charles E. Williams, M.A., M.B., Indian Medical Service. Communicated by Dr. David Sharp, M.A., F.R.S.

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This Mantis, of which a living immature specimen is exhibited, is found in many parts of Central and Eastern India, in Bengal and the Central Provinces and Madras, in Ceylon, and in Lower Burma.

The appearance and habits of the immature insect were described by Dr. J. Anderson to the Asiatic Society of Bengal in 1877 (*vide* Proc. Asiatic Society of Bengal, 1877, p. 193). His description, which is rather meagre, is quoted at length in the "Cambridge Natural History" (Insects), vol. v, pp. 254–257. So far as I am aware, no full account of its Life History and habits has been published hitherto.

The following account is compiled from my own notes made during a period of nearly two years, during which I kept numbers of these insects under observation, and watched their development from the egg to the adult form.

Owing to their retiring habits and protective form and coloration, they are extremely difficult to find when searched for. Although I have reason to know that they are not uncommon near Rangoon, no European of my acquaintance had ever seen this species in Burma. However, both De Saussure and Brunner von Wattenwyl mention Pegu (*i. e.* Lower Burma) as its habitat.

The chief distinctive external characters of the insect consist in the peculiar modifications of the prothorax, and in the leaf-like expansions of the lateral margins of the dorsal abdominal plates, and those of the distal extremities of the femora of the two hind pairs of limbs, together with the elongated bifid cephalic crest.

These special characteristics are found to be more or less developed in other members of the tribe Empusides, but

in no other species has the modification of the tribal type taken precisely the same lines as in *Gongylus*.

The prothorax is elongated into a narrow stalk, leading to a somewhat diamond-shaped or disc-like expansion at the insertion of the front pair of limbs (raptorial limbs). This disc is coloured on its ventral aspect a brilliant azure-blue, the angles and margins of which may be more or less tipped with a warm purple hue. In the centre of this disc is a deeply pigmented black spot triangular in shape. Closely correlated with this colouring and formation is the attitude adopted by the insect. When at rest and feeding it hangs head downward, the ventral surface of the thorax and prothorax being turned skywards and the dorsal surface towards the ground. The azure-coloured disc is thus turned towards the brightest part of the sky, or preferably towards the blazing sun all through the hours of daylight, and this part of the insect assumes the appearance of a blue flower, by which other insects, the prey of the Mantis, are attracted to it; this deceptive effect is enhanced by the stalk-like elongation of the prothorax, by the black central spot, which it has been suggested mimics the opening of the tube of a corolla, and by the gently swaying movements of the insect from side to side, as if it were a blossom agitated by the breeze. The dorsal aspect of the prothorax, and the dorsal surface of the insect generally, and all other parts of the ventral surface, except the prothoracic disc, are varied in colour, and marked by bands of black pigment on a ground of light or dark brown, and here and there by green markings, and this more sober colouring is adapted to conceal the Mantis both from its prey and from its possible enemies.

The female, on passing to the winged stage, develops a relatively small pair of wings and of tegmina. The former are too small for flight, and the tegmina, which do not reach so far as the posterior end of the abdomen, are greatly modified to resemble dead and shrivelled leaves. The female is therefore to all intents and purposes wingless.

The adult male on the other hand is more slenderly built, and has large wings adapted for powerful flight. The wings and tegmina both reach some distance behind the posterior end of the abdomen, and they are handsomely ornamented by oblique black lines, not unlike the marking on the tegmina of some species of Harpagides. The adult

male has long bi-pectinate antennæ, gracefully curved; while the antennæ of the female are short, hair-like, curved outwards, with fine rounded hooks at the free end, and never reaching beyond the tip of the cephalic crest. The prothoracic disc is in the male narrower and more diamond-shaped than in the female, which is altogether a more heavily-built insect in association with its sedentary habits. The male adopts the same habits as the female for catching its prey.

These insects are found hanging from creepers and the foliage of trees and shrubs in country lying high and well drained; also the female adult was found on hay-grass about eighteen inches high. I met with two groups of half-grown nymphs on creepers in my own garden. There was a difference of colour in the two groups, the one was of a light warm brown ground colour, while the other was of a sooty hue. The markings of both varieties appear to be similar, and the same male interbred with both varieties of females. Their colours were inherited by the offspring. The specimen shown is of the darker variety.

Food.

When feeding the insect invariably holds the fore part of the prothorax towards the brightest light available at an angle with the body of between thirty and forty degrees; insects are frequently captured and are generally devoured entirely, with the exception of the wings and some of the legs. The favourite food of the adult insect and of the larger nymphs consists of small lepidoptera; chiefly of a Skipper closely allied to, if not identical with, the British Dingy Skipper. This butterfly abounds on the creepers and flowering shrubs frequented by *Gongylus* during the period when the Mantis is preparing for its last ecdysis, viz. towards the end of the rainy season in September and October, and on till the end of December. Much larger butterflies also, including *Papillios*, are captured by the adult insect. The nymph is of a retiring nature, and hides all but its prothoracic disc and stalk behind the foliage, while the adult insect displays its whole body and limbs at the end of a twig or spray, or on a spike of flowers. It maintains this inverted position exposed to the full sunlight without any serious risk from its enemies, being evidently protected by its peculiar colouring and form. I have noticed large nymphs of *Gongylus* living for days and

weeks on sprays frequented by lizards of all sizes and remaining unhurt. The large Calotes lizards are dangerous enemies, and when the leaves fall from the bushes during the hot dry weather of February and March the Mantis frequently becomes the victim of this lizard, which climbs the stem of the bush from below and comes upon the Mantis from behind. It will be noticed that the protective coloration and markings of the dorsal surface of the Mantis, which is turned downwards, are very elaborate, as if to conceal it against a possible foe advancing from that direction, whence indeed the lizard usually comes. In seizing the Mantis Calotes usually bites through the prothoracic stalk; the fore part of the insect bearing the disc and the spiny raptorial limbs and head, falls to the ground, while the more fleshy thorax and abdomen are ingested. The tough exoskeleton of these parts is easily digested by the gastric juice of the lizard.

It may be added that the Mantis does not necessarily frequent native plants, or those having blue blossoms; it may be found alike on exotic or on indigenous plants, and on floral spikes bearing blossoms of any other colour. It appears to be just as attractive to insects in these situations as if it were on blossoms of its own colour.

When irritated or alarmed by the close approach of some threatening object, or of an enemy, this Mantis adopts a very curious defensive attitude. The raptorial limbs, which are usually held folded together in front of the prothoracic disc, are now widely separated until they lie in the plane of the disc, the inner aspect of the coxæ being directed forwards; the femora and tibia remain folded upon them as before. It is now seen that the internal aspect of the coxæ is coloured a brilliant purple, dotted over with circular white or pale blue spots, and the femora have a warm red-brown coloration on this aspect. The effect produced by this coloration and by the blue prothoracic disc showing between the separated coxæ, is that of some curiously-shaped and brilliantly-coloured orchid. If the irritating object, *e. g.* the finger or point of a stick, approach too near, the Mantis strikes furiously at it with its fore limbs repeatedly and with lightning-like rapidity. This hostile attitude is shown by both immature and adult insects, and is first exhibited by the nymph when the coloration of the prothoracic disc and anterior coxæ is matured, *i. e.* about the end of the third month of pupal

life. The attitude is plainly associated with the peculiar coloration. I have no doubt that even a large lizard would be deterred from seizing the Mantis, if confronted by it in this manner. I have seen it adopt this attitude only when some large beetle, butterfly, or hymenopteron investigated the floral expansion; but on these occasions it did not strike out at the intruder, but contented itself with an exhibition of the warning or hostile colour-effect. I never saw wasps or bees captured by this Mantis, but small beetles and hymenoptera are frequently seized.

When adopting the hostile attitude described, the Mantis sways the whole body rhythmically to and fro. If in the adult stage, the tegmina are raised slightly and spread outwards and ventral-wards, until their outer edges, which are serrated, come into contact with the femora of the hinder limbs; the lateral movements of the body then give rise to friction between the tegmina and femora, and a hissing sound is thus produced; the wings are slightly spread over the abdomen, which is distended. In the nymph, which has the abdomen curved over the thorax, so that its dorsal surface looks ventral-wards, in the same direction as the prothoracic disc, a still more astonishing phenomenon is exhibited in association with the hostile attitude of the fore limbs. The abdomen is greatly distended, and both widened and elongated; upon the larger segments broad bands of a bright purple colour, and on the narrow hinder segments a large black eye spot, are developed. This remarkable effect is produced by the elongation of the abdomen bringing into view portions of the segments, including the delicate inter-segmental membranes, which are usually hidden from view. These are naturally coloured purple or black according to their serial position. It is possible that under excitement this purple coloration of the deeper-lying tissues may be actually increased in some way, but this is doubtful. The insect when dropped to the ground will often feign death for a short time, lying on its back with its limbs contracted above the thorax as after real death.

I will now trace the life history of the insect beginning from the attainment of the winged stage. The nymph effects its last ecdysis in the middle of October, and the winged males appear among the females a fortnight or three weeks later. Within twenty-four hours of fertilization the female commences to form its first egg-case.

Mid-day is chosen for this work. The insect retires from its usually exposed position to within the shelter of the foliage, and constructs the egg-case on a branch of the bush near the stem, or on the stem itself. If on a branch, it is always placed on the under-side, and constructed from the stem outwards towards the periphery of the bush. If situated on the stem it is formed from below upwards. The insect, having taken up her position, proceeds to pour out secretions from the accessory genital glands, with which she builds up the ootheca. These secretions appear to be of two kinds; the one is a thick viscid semi-transparent fluid which very rapidly hardens to the consistency of horn; the framework and nearly the whole bulk of the structure is formed of this material, and the eggs are extruded and placed in rows, with their long axis vertical to the branch on which the ootheca is built. The second secretion is thinner in consistency, and as it pours out is beaten up into a white foam or lather-like mass, by the very rapid rotation of two small spatulate organs which are protruded at the sides of the genital orifice. This lather-like substance envelops the egg at the moment of extrusion, so that the manner in which it is placed in a position at right angles to that it occupies during its exit from the oviduct cannot be made out. As the eggs are placed in position the lather is constantly being swept aside by the end of the abdomen until it occupies a position on the outside of the ootheca, which it entirely clothes throughout to a depth of $\frac{1}{8}$ of an inch. Its function appears to be, in the first place, to protect the egg from parasitic insects until it is firmly placed in its matrix, and secondly, as an outer covering to the ootheca, to shield its contents from the direct rays of the sun and from the desiccating effects of the hot air. The lather is full of air-bubbles, and at first is sticky, adhering to the fingers like bird-lime, gradually changing to a firm spongy consistency. It is quite tasteless and free from odour. It no doubt protects the ootheca from the depredation of possible foes. I have frequently noticed a small parasitic hymenopteron sitting upon the exterior of the egg-cases, but have never hatched out any from them. A small black ant, however, circumvents the measures taken by the Mantis for the safe protection of its eggs by boring into the egg-case between it and the bough to which it is attached, and robbing it of its eggs and their contents. The ootheca is roughly square in section. The

eggs are arranged in a single layer, four abreast, and are usually about forty in number. The viscid secretion which forms the matrix of the case hardens with remarkable rapidity, so that even a few seconds after the egg is laid it is not possible to dislodge it with the point of a knife. It may be that the lather-like secretion has the function of protecting this fluid from the hardening effects of the atmosphere while the egg is being placed in position.

It may further be noticed that the female uses her cerci which are attached to the last ventral segment, in the manner of a pair of callipers to shape her egg-case and to arrange the lather-like substance in regular parallel rows along its exterior, corresponding in position to some degree, with the rows of eggs within.

The ootheca is finished off at either end with a sort of rostrum formed by a vertical plane of matrix substance projecting in the middle line of the structure. That formed at the commencement of the construction is short and rounded, while that formed at the end of the process is drawn out into a sharp point, as the insect moves away. These rostra are covered with the lather, in the same way as the rest of the ootheca. Each female makes about five of these egg-cases during four or five weeks; a single union with the male appears to suffice for the fertilization of the whole series of eggs laid in the season. The act of forming the egg-case occupies about an hour. The incubation period occupies from forty-four to forty-eight days. The young nymphs in one ootheca hatch out almost simultaneously. The embryos are developed in the egg with their heads pointing towards the free surface of the ootheca, on the side opposite to its attachment to the branch. In some way the embryo softens the end of the cell in which it lies, and this falls outwards as a small disc hanging by a silken thread, and setting the nymph free. At the moment of hatching the nymphs come pouring out of their cells, and hang each by a silken thread suspended in the air; this silken thread is not attached to the cerci, which have not, I think, the function of spinnerets as figured for another species by Brongniart. The thread appears to be a single one of twisted strands, and to be attached at one end to the silk lining of the egg-case, and at the other to a very delicate silk membrane which enfolds the body of the nymph. The nymphs, clad in this membrane, have a distinctly maggot-like appearance.

They soon free themselves from this covering, which remains hanging from the ootheca, and enter upon an independent existence within a quarter of an hour of hatching. At birth they are a tallowy-white colour with the exception of the limbs and prothorax, which are a pinkish-brown colour. This white colour is changed for a brown hue very shortly, about twenty minutes after hatching. The nymphs having freed themselves of their investing membrane at once proceed to climb upwards until they reach the extremity of the branch, where they take up their position for the rest of their pupal existence on the under-side of a leaf or twig. They resemble the full-grown nymph in shape from the moment of hatching, and adopt the inverted position at once. At first they have a hairy appearance, but a lens shows this to be caused by the keel-like expansions and edges and angles of the dorsal and ventral plates, which are relatively exaggerated in the minute nymph.

The nymphs undergo eleven or twelve ecdyses between the date of hatching and the change to the imago stage. The period between ecdyses is, in the early stages, from eighteen to twenty days—and in the later months this period appears to be prolonged to twenty-eight or thirty days. I believe that the nymph effects its escape from the egg-case by the expansion and peristaltic writhings of its abdomen, and not by any hair-like projections of its cerci and limbs as is stated by Trimen in the case of another species. The limbs indeed are twisted up together like a bundle of string, and they and the exoskeleton are quite soft, and could not be used to assist the escape from the egg-case; moreover the nymph is enclosed in a silken shroud, clad in which it emerges from the egg.

The act of ecdysis deserves a short description. The night or early morning is usually chosen for this function, for until it is complete, and perhaps for half-an-hour after, the soft succulent body of the nymph is liable to be seized by one of its comrades, who practise cannibalism for the first few months of free existence, and devour each other readily if a favourable opportunity occurs, or by other foes, spiders, wasps, etc. Before commencing the change the nymph retires to a dark nook behind dense foliage and attaches itself to its support by the terminal claws of all its six legs, which are bunched together, the antennæ are also brought into line with the limbs, and the abdomen is

straightened and curved ventral-wards till it lies beside the limbs; the skin then splits along the dorsal side, and the prothorax emerges as a loop, the head flexed upon the ventral side of the thorax is drawn out followed by the antennæ, and the pairs of legs in serial order; lastly, after the limbs have regained a hold on their support, the terminal extremity of the abdomen is freed. At this stage the insect is quite white, and has a bloated appearance owing to the great size of its abdomen, which is twice that which it will assume later, when curved dorsal-wards; even the eyes are covered by a white film, and only the narrower joints of the legs and the prothorax are coloured a pinkish-brown; after a few minutes the return to the ordinary shape and coloration is effected. The above process is repeated at each moult, and is substantially that which the newly-hatched nymph undergoes when freeing itself from the enveloping egg-membrane. The distention of the abdomen throughout the act, possibly with air, seems to play a very important part in freeing the insect from its discarded skin.

Colour Changes.

At birth the prothoracic disc is relatively small and inconspicuous. It is a greyish-white colour on its ventral aspect, and the central black spot is absent. The azure colour is only fully developed at the seventh moult, five months after hatching, and the purple coloration of the internal aspect of the coxæ, and the purple and black bands on the dorsal surface of the abdomen become well defined about the same period. These colours are however faintly indicated earlier than this, after the second moult. The ground colour of the young nymphs is for the first moult or two a greyish-brown, after this the nymphs are very variously coloured, either light grey, brown, black, pink, or light or dark red. The whole body of the nymph assumes one general colour, the markings observed in the later stages being faintly indicated.

Mr. Shelford, in "Notes on Bornean Mantises," contributed to the "Zoologist," 1903, states that the young of *Hymenopus bicornis* have the power of adopting the colour of their surroundings at the time of moulting; thus they take the colour of a blossom on which they may be sitting. I did not carry out any experiments in this direction with the young of *Gongylus,* but it is very

probable that, as they have the power of producing such a variety of colours, they may also possess that of assimilating their coloration to that of their environment. I hope to be able to test this faculty on a future occasion.

After the fifth month the nymphs remain a light or dark brown, and appear to have lost the power of varying their ground colour. The development of the black spot in the centre of the prothoracic disc is a phenomenon of special interest. As already stated, this is absent at birth. At the first ecdysis, which takes place eighteen days after hatching, it may be noticed that a portion of the pigment around the posterior angle of the disc, on its ventral aspect, becomes separated from the lateral portions, which later disappear. The middle portion, really formed of two dots one on each side of the middle line, is advanced centripetally at each succeeding moult, until at about the sixth moult it reaches the centre of the disc. It retains permanently its angular shape as an indication of its origin. The attractive influence exercised by this intensely black spot for the insects which form the prey of *Gongylus* is enhanced by the total disappearance of all other black pigment from the disc. An interesting comparison may be made in this connection between *Gongylus* and the large African Mantis, *Idolum diabolicum*, which is closely related in form and habits to it. In the latter insect the dark pigment at the posterior margin of the disc is retained throughout life, but there is no central black spot, and this species does not use its prothoracic expansion for the purpose of floral simulation, but has it coloured to resemble the foliage amidst which it conceals itself.

The nymphs at the time of hatching measure from $\frac{9}{16}$ to $\frac{11}{16}$ inch in length, and increase by about one-quarter of their length at each moult. The adult female measures four inches from tip of cephalic crest to the posterior extremity of the abdomen. The young nymphs feed mainly on mosquitoes; they will only take live victims on the wing, and will not touch dead mosquitoes or those seated motionless in their midst. At all stages the Mantis is fond of water, and in captivity will die if this is not sprinkled over it frequently. After the second moult house-flies are eaten, and a month or so later bluebottle flies are captured. When walking and climbing *Gongylus* uses the tarsi of its fore limbs as well as of the two hinder pairs. If the tarsi of the fore limbs are damaged it assists itself by the large tibial claw,

but the main functions of this claw are for the seizure of prey and for defence. The loss of a limb of either of the hinder pairs is repaired at the next moult, but the newly-developed limb is smaller and weaker than the original. The more complex raptorial limbs are not reproduced, although the tibial claw and the tarsus may be. Often a joint or so of the tarsus is missing in the newly-formed limb, but the terminal pair of tarsal claws is always present.

The Development of Sexual Characteristics.

Immediately after the nymph is hatched one notices no distinction between the two sexes. They can be distinguished at this stage by microscopical examination of the terminal ventral plate, the posterior margin of which is deeply notched in the middle line in the female, but straight and uninterrupted in the male. This character persists throughout life.

At the third ecdysis the antennæ in the male are considerably longer than in the female, but in both sexes they remain hair-like, and are curved into a rounded hook at the free end, as in the adult female.

At the ninth moult the male antennæ become greatly thickened for the basal three-quarters of their length, while the remaining quarter is straight and finely tapering. The bi-pectinate form is not assumed until the imago stage. At the fifth moult the female is obviously larger than the male, and this relative size is maintained for the rest of life. About the same time the prothoracic disc of the male assumes its characteristic shape, being smaller, narrower, and more perfectly diamond-shaped than in the female.

Comparison of the habits and mimetic characteristics of Gongylus *with those of* Idolum diabolicum.

This large African species is most closely related to *Gongylus* in its habits and conformation. For a description of the insect the reader is referred to the article by Dr. D. Sharp in Vol. X. of the Proceedings of the Cambridge Philosophical Society, where a coloured sketch of the ventral aspect of the insect is given; this shows that the floral simulation is effected by the petaloid colouring of the inner aspect of the greatly expanded coxæ of the first pair of legs, which is a brilliant purple; and the coxæ are

widely separated, the limbs being extended in front of the head, while the insect maintains a more or less inverted position of the body, with the ventral surface turned towards the light.

The females possess well-developed wings, and have the power of flight. The large prothoracic expansion is coloured a faint green, and has no central black spot; it plays no part in the floral mimicry. Here we see the petaloid colouring, which is confined to the prothoracic disc in *Gongylus*, appearing in another situation, viz. on the coxæ, in *Idolum*, and that in *Gongylus* the purple colouring of the coxæ is utilized for quite a different purpose, to produce a hostile or warning effect. We may remark that *Gongylus* when adopting a hostile attitude not infrequently opens out the several joints of its fore limbs, though not so widely or so far in front of the head as does *Idolum*—and it is worth recalling that Mr. Shelford of the Sarawak Museum, in the paper before referred to, states that many Bornean Mantises so extend their raptorial limbs before seizing their prey. He calls this attitude that they adopt a "warning" attitude. The hostile attitude already described in *Gongylus* is probably deserving of this name, since it evidently seeks by such action to drive off an unwelcome visitor, but the term is not perhaps so well applied to an act in other species which precedes an attempt to seize the prey.

Floral simulation by Mantises appears to have proceeded along two distinct lines. In the majority of species, including some species of the tribe Empusides, the mimicry depends upon the coloration and conformation of the wings and tegmina and of the dorsal aspect of the body, correlated with special attitudes adopted to display these peculiar markings to advantage. Such coloration and modification of form may also be developed in connection with a warning or hostile attitude. A large, winged Mantis, species unknown, found in the Shan States, which has large eye-spots and brilliant colours on its wings, spreads out and displays these when adopting a hostile attitude, perhaps also as a means of attracting its prey, though this has not yet been observed.

The second line of floral simulation is that taken by *Gongylus* and *Idolum*, in which species the ventral aspect is modified in form and colour, chiefly with a view to attraction of prey, while the dorsal surface and wings are

free of conspicuous colours and markings. In all these insects one is struck by the recurrence of the peculiar purple pigment for the production of petaloid colouring in various parts of the body. Dr. Sharp, in the article on *Idolum* already referred to, has some useful remarks on the distribution of this pigment in Mantises. In other Orthoptera a purple or crimson coloration of the wings and other parts of the body is not uncommon, and a similar pigment occurs in other Orders of insects, *e. g.* Hemiptera.

The azure blue pigment of the prothoracic disc in *Gongylus* is probably related to the purple pigment found in other parts of the body, for it tends to change slowly to purple, especially around the margins. One of my Mantises when dying exuded a bead of purplish fluid from its mouth.

I had hoped to find in a study of the life history of *Gongylus* some indication which would throw light upon the peculiar inverted position which it adopts, and for which it is specially modified. No suggestions have however been derived from my investigations. At its exit from the egg the nymph has already the form of the mature insect, and the special coloration is produced as soon as the insect is large enough for it to be of any value in its economy. Many other species may be found occupying temporarily an inverted position when lying in wait for prey, but with the exception of *Gongylus* and *Idolum* I know of none which is specially modified to this end. Fuller information is required as to the habits of many other species than is at present obtainable. The specimens of dried Mantises available for study in our museums give but little indication of the interesting and varied phenomena which the insects exhibit during life.