PHENGODIDS: Giant Glowworm Beetles

(A Taxonomic Survey of Lanterns and their Use)

(continued from Companion 1)

We will look into explanations for the phengodid peculiarity of subterranean light after introducing our North American giant glowworm fauna. The most commonly collected species belong to the widespread genus *Phengodes* and the western/southwestern genus *Zarhipis. Euryopa* is a less known member of the same tribe, the phengodini. The obscure ranks of the tribe Mastinocerini consist of seldom seen and little known genera such as *Cenophengus, Paraptorthodius, Distremocephalus* and *Mastinocerus.* Due to the variety of forms within populations, the number of North American species is open to debate. In *Zarhipis,* there are at least three species. *Z. integripennis* is the most widely distributed species, being found in western Washington and Oregon, throughout California to the southern half of Arizona and Baja Mexico. In Arizona it is restricted to mountains and appears to favor somewhat moister regions than *Z. truncaticeps,* which is a desert dweller, found in Arizona, California and New Mexico, and possibly southwestern Texas. *Z. tiemanni* is most abundant in the China Lake district of California, but has been collected in Nevada and Arizona as well.

Among *Phengodes*, *P. mexicana* is known from Arizona, New Mexico and Durango. *P. arizonensis, inflata* and *fenestrata* are likewise western and southwestern species. *P. fucipes* inhabits both sides of the Mississippi River. *R. plumosa* lives in the east and Midwest, from Ontario to Georgia and New York to Nebraska. *P. nigromaculata* is a southern native. Larvae are a pale cream and brown color like those of *R. plumosa.* The geographic range of *R. laticollis* overlaps those of nigromaculata and plumosa, but laticollis is a much larger insect. The larva is black with orange blotches.

As far as anyone knows all glowworms are specialized hunters of millipedes. There is a 19th century record of a Texan *Distremocephalus* (= Mastinocerus) larva subsisting on small snails, but since mollusks are a typical prey of firefly larvae, this may have been a mistaken identification. The detailed observations of the late Darwin Tiernann on *Z. integrepennis* are similar to what I have seen of millipede stalking and killing by *Phengodes laticollis* and *nigromaculata* and suggest a long and close evolutionary relationship. A larva "races" alongside a millipede much larger than itself, mounts its back, and then coils around it. It stretches full length, and reaching the vulnerable neck articulation, severs the main nerve. Both *Zarhipis* and *Phengodes* will drag their bulky trophy underground, where they remove the head. A larva then pushes its own head into the wound and eats its way into the body cavity, sometimes entirely disappearing into the hollowed-out "shell." It can take days for a glowworm to complete its meal.

All stages of the phengodid life cycle bear lights. Embryos can be seen glowing inside the egg and the larvae and larviform females sport multiple light organs, the pattern varying somewhat among species. In *Zarhipis* and *Phengodes* there are points of light on the sides of the second through twelfth body segments and stripes of light shine between the segments. One species of *Phengodes,* whose identity is not yet confirmed, has a double row of lights down its belly. *Mastinocerus opaculas* has two very large lights on the head with much smaller and dimmer organs glowing along the abdomen. Pupae are also luminous and while the light pattern is larva-like, its intensity is greater. North American males are generally not well lit. I have seen *P. laticollis* suffused with a greenish glow that gradually dims and expires over the insect's brief life. *Zarhipis* males have a feeble luminescence that requires allowing the eyes to become dark-adapted before it can be seen. *Cenophengus ciceroi,* from Arizona saguaro country, has faint green spots on the tip of the abdomen that glow continuously. However, an early description of a male *Distremocephalus texanus* with conspicuous lights in the head and tail sounds more prepossessing.

The value of luminescence to a beetle larva is a mystery. It is particularly puzzling when the larva lives and glows underground. A number of reasons for carrying lights have been proposed, but the first one to consider is aposematism" or "warning coloration." The great 19th century naturalists, particularly H. W. Bates, pointed out that some insects were distasteful to birds and other predators and that poisonous species often "advertise" their unpalatability with bright warning colors. The familiar Monarch butterfly contains cardiac glycodide heart poisons and its bright orange and black wings stick in the memory as well as in the craw of a bird that eats one — and later vomits it up. A few such trials will cause a bird to avoid Monarchs and butterflies that look like Monarchs. In addition to orange, red (as in lady bird beetles) and yellow (as in wasps) are used to advertise nauseous secretions and venoms, the same colors found in eye-catching traffic signals. The brighter and more obvious an animal is the earlier a predator will take note and the less likely it is to complete an attack that would have a bad effect on both participants, In some cases, then, it pays to be noticed.

A light in the dark is very noticeable. If this obviousness could be coupled to evidence of a potent defense, then warning coloration could be a plausible explanation for luminescence in phengodids. Unfortunately, the rarity of phengodids makes it difficult to experimentally test the idea. However, there is indirect evidence of defensive chemicals. When handled, *P. laticollis* secretes copious amounts of yellow fluid that quickly spreads over the entire insect. Once I put one in a cage with a large centipede that it attacked but did not eat, though the predator immediately afterwards ate a large mealworm. When roughly handled, *Z. integripennis* secretes a clear amber fluid from U-shaped pores on abdominal segments 2-9. *Phrixothrix,* a Latin American genus, discharges an irritating reddish oily substance from the anus when disturbed. It will turn the end of its body towards its attacker and swing it from side to side while ejecting its anal fluid. A collector bitten on the hand by a *Phrixothrix* larva noticed a brown substance on the wound and the surrounding skin remained inflamed for several days. The Old World tropic genus *Rhagophthalmus* has a caustic odor. All of this at least suggests a chemical defense that might be advertised by phengodid glows. A bit of circumstantial evidence is that the lights of many glowworms brighten or light up when the insect is disturbed. They may be intensifying their warning as danger approaches — just as a rattlesnake may increase the frequency of its buzzes.

Even if phengodids pack a potent chemical punch, could a warning signal that can't be sent through the surrounding soil be of any use? Well, yes it could, if it were the first thing a burrowing predator saw as it broke in upon its prey. To insure being noticed an underground light display should be spread over the surface of the insect. Phengodids tend to have numerous light organs dispersed over their bodies. *Phengodes* and *Zarhipis* species have already been described. Among tropical genera there are some spectacular variations. Besides 11 pairs of thoracic and abdominal lights, *Rhagophthalmus* has large firefly-like taillights, as does *Dioptoma adamsi. Diplocladon hasselti* bears a line of lights down the middle of its back as well as blue-green lights on the sides of every body segment except the head and tip of the tail. *Phrixothrix* has rose-red

headlights and yellow-green lights from the middle of the thorax to the ninth abdominal segment. The light arrangement is similar in *Stenophrixothrix*, headlights plus lateral spots on the last 8 abdominal segments, though their lights are yellow-green in color throughout. *Ceratophengus* is much like *Stenophrixothrix*, but some *Mastinocerus* possess headlights and a row of 9 lights down the middle of their back. In an undescribed and colorful Brazilian species, the headlights are orange and the body lights yellow. *Ceratophengus* males are reported to have a pair of lights on their head and another pair near the tip of their tail, while *Dictenum* males bear greenish-yellow light organs on each body segment. In sum, Phengodids are well lit, all over.

Besides being spread out, a subterranean signaling system should be on a lot of the time. There may be little warning of an unseen predator's attack. It would be better to signal continuously so as not to be literally in the jaws of death before giving your luminous warning. Many Phengodids spend most or all of their lives illuminated.

Of course, all of this argument about warning lights and chemical warfare is educated guesswork. The naturalists who will invest the energy and time to watch phengodids and design experiments to discover why glowworms glow may not as yet have turned over their first log or lifted their first spade of soil. There is much work that could be done by the patient amateur. But, before leaving the always-agreeable land of "maybe," there is one more luminous landmark to visit the *Phrixothrix* species. Latin America's wonderful "railroad worms" have two colors of light, some of which are set in unusual locations. Lights on the heads of beetle larvae are rare, occurring only in a handful of phengodid genera. Red-colored lights are very rare. Only *Phrixothrix,* the mysterious "Astraptor," found once on a Guatemalan streambank, and a few as yet undescribed Brazilian species have red glows. However, in all the cases where there are both headlights and red lights, the headlights are red! When two peculiar things occur together it is tempting to suspect that they are related. In the world revealed by the invertebrate eye the color red has one unusual feature; it isn't there. Most arthropods cannot see red light. But what if a predatory species could both emit and see by a light that its prey could not sense? Then it would stalk victims illuminated by invisible beams and ignorant of their danger. Astraptor's light shines in a direction consistent with this view. Its collector noted that its ruby light was not easily seen from above and was best observed reflecting from objects in front of it. If red lights are killing lights in the Phengodidae, then they might have a parallel in the red photophores carried by the deep-sea fish *Pachystomias* behind its eyes. Since nothing is simple, least of all bioluminescent animals, it should be noted that Dr. Chabora of the University of Sao Paulo has recently discovered a new glowworm in the and savannas of Brazil. Unlike *Phrixothrix,* which has a red light in the head and yellowish-green lights along its body, this new species has red lights all over! It does not seem likely that abdominal lights are used for self-illumination, but then the Phengodidae are an unlikely bunch.

Light and love entwine in some luminous organisms. Fireflies are very well known examples of this; however, the role of luminescence in phengodid mating is not always clear. Some males, like those of *Diptoma adamsi* with their scattering of 26 emerald green lights, become brilliantly lit when sexually excited. Both male and female *Phrixothrix tiemanni* luminance while coupling in burrows. A luminous organ on the abdomen of the *Stenophengus* male is backed by a white reflector like that found in some fireflies. Such a specialization would seem to be an adaptation to increase the efficiency (range/cost) of a broadcast signal. As discussed earlier, our North American males are less photo-endowed. They usually glow weakly and only for a short time. It seems they are less likely than their tropical relatives to be broadcasting sexual messages. But it is important to remember that only a few of our native species have been seen mating and those only rarely, so no one really knows what sort of fireworks may take place under the right conditions.

Female phengodids have the same compliment of light organs as the larvae, but females are often more brightly luminous. Lights could supplement chemical sexual signals females emit to guide potential mates. Female glows might be particularly important in genera such as *Dioptoma,* in which males have large eyes and much-reduced antennae. In others, such as our native *Zarhipis* adult females, lights probably continue to function for the same reason that they shine in the larvae… whatever that may be! Males have small eyes and mating occurs in daylight.

The following are papers someone with an interest in phengodids can refer to for More detailed information. Notice as you read how little is known and how nearly every careful observation will be of interest to your fellow naturalists. Just this year I have found new light organs on one of our most common species and finally discovered the millipede prey of another. (John Siviniski, USDA Gainesville)

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