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BIOLOGY OF RIFFLE BEETLES

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INTRODUCTION

What are riffle beetles? This question is not new to me, nor is it unexpected, even when it comes from an entomologist. No formal designation has been proposed for the use of this common name, but many of us have unofficially adopted the term "riffle beetles" for the aquatic dryopoid beetles that typically occur in flowing streams, especially in the shallow riffles or rapids. Unlike the familiar and conspicuous water beetles such as dytiscids, gyrinids, and hydrophilids, riffle beetles do not swim and do not come to the surface for air. Most of them are slow in their movements and cling tenaciously to the substrate. Most are also quite small, about the size of household ants, although giants among them exceed the dimensions of a housefly. Some aquatic biologists restrict the term "riffle beetles" to members of the family Elmidae, or even to the subfamily Elminae, but in this review I also include the riffle-dwelling members of the family Dryopidae, the genus *Lutrochus* (Lutrochidae, formerly in the family Limnichidae), and the water penny beetles (family Psephenidae *sensu lato*). Most attention is devoted to the elmids, which are represented by the greatest numbers of both species and individuals.

All elmids are aquatic as larvae. Adults of the subfamily Elminae and of some Larinae live and feed underwater, often alongside their larvae. Among the Dryopidae, the known larvae are mostly terrestrial or semiaquatic, as are the adults of many species (4, 10, 14, 16). Only the adults of *Helichus* would qualify as familiar riffle beetles, but those of *Elmoparnus* deserve mention as interesting neotropical rarities (20, 95). All Psephenidae are aquatic as larvae; the adults are usually riparian or terrestrial.

The small, dermestidlike limnichids are associated with water and are frequently abundant at or near the water's edge, but I am aware of none that

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inhabits streams except *Lutrochus* and close neotropical relatives, which Crowson (36) puts in a separate family, the Lutrochidae. I heartily agree that they merit separation. Paulus (79) has described the terrestrial larvae of two European genera of limnichids, and I have examined those of two American genera; they bear little resemblance to the larvae of *Lutrochus* (22, 49, 112).

Of the remaining families placed by Crowson (36) in the superfamily Dryopoidea, I omit the Eulichadidae because I have never found them in riffles and am unfamiliar with the group. Among the ptilodactylids, the larvae of *Anchytarsus* inhabit riffles, but I don't think of them as riffle beetles; I shall leave coverage of these to LeSage & Harper (65) and Spangler (93) (ecology and life history), and to Stribling (100) (systematics). Spangler (90) also spares us the trouble of considering the Chelonariidae as "almost" riffle beetles. Both larvae and adults of Heteroceridae are closely associated with water (62, 78), but are not aquatic, and are definitely not riffle dwellers.

I outline the life histories of the groups covered and discuss their means of remaining permanently underwater, some aspects of their ecology, predators and parasites, and something of their past history. In no case is my treatment exhaustive. Perhaps it is most extensive in least-known subject areas.

LIFE HISTORY

Elmidae

ELMINAE Members of this subfamily are the most completely aquatic of all beetles. Little is known of courtship behavior, but it seems minimal. Although there is nothing unusual about mating in most elmids, copulating pairs of *Zaitzevia* are so firmly attached they commonly remain linked when preserved or dried and pinned.

The female genitalia include sensory styli used in selecting oviposition sites. Few observations of elmid oviposition have been reported (67, 111), but it is probable that most elmids glue their eggs singly or in small clusters to the undersides of submerged rocks, wood, or plant stems, depending upon habitat preference of the species.

Incubation time is rather short (5–15 days), varying with the temperature. Duration of larval stage (6–36 mo) and number of instars (5–8) also vary with temperature, as well as with body size and available food. Development is faster at higher temperatures; northern populations of a given species may require an additional year in the larval stage. Other factors being equal, small beetles need less time to develop and exhibit fewer larval instars than large beetles (7, 8, 59, 67, 74, 87, 111).

Mature larvae pupate in protected sites above the water line. They use various strategies to get from larval habitat to pupation site; direct crawling, if feasible, is the simplest method. Streams in which the water level fluctuates provide another opportunity, as demonstrated by White (111) and confirmed by Seagle (84); mature larvae simply wait in the shallow water at the stream edge until the water level drops, allowing them to pupate in situ. One result of this pattern is relatively synchronized emergence of adults.

Drifting is a widely used means of transport among stream insects (12, 30, 60, 77, 82, 107, 109). Larvae can drift from midstream to a snag or boulder upon which to crawl out. Perez (80) was the first to report larval drift of elmids and to suggest its mechanism, although he noted it simply as a device for escaping poor environmental conditions such as water with low dissolved oxygen. Mature larvae develop tracheal air sacs that can be compressed or expanded by contraction or relaxation of tergo-sternal muscles, respectively; these provide a cartesian diver system for controlling the specific gravity of the body (41, 96, 102). The fact that air sacs do not occur in earlier instars suggests that their primary adaptive function is probably for transport toward pupation sites rather than simply for the search for greener pastures or less foul water.

Having found a satisfactory site in moist sand, humus, moss, or the like, the prepupal larva proceeds to form an ovoid cell or chamber by appropriate body movements. Xylophagous larvae such as *Macronychus* usually pupate in rotten wood or beneath loose bark (8, 66, 67). In temperate zones pupation commonly occurs from late spring through summer and requires 1–2 wk. In tropical regions where there is no pronounced dry season, pupation occurs throughout the year.

Following eclosion, commonly at dusk of the first warm and humid night, recently emerged alate elmids take flight. This is their only dispersal flight. At this stage they are capable of surviving for several days out of water (84, 111). Many species are positively phototactic, to the delight of coleopterists equipped with light traps. In fact, some species and even genera are known only from light-trapped specimens, and are only presumed to deserve the appellation "riffle beetles" (38, 91). Collectors are understandably pleased with light-trapped material, not only because great numbers may be taken with minimal effort, but also because the specimens are cleaner than those collected from streams. (In some mineral-laden streams, elderly elmids may become so encrusted that their stony armor far outweighs the beetles themselves.) Some species are presumably always flightless, e.g. those that inhabit warm springs, such as *Microcylloepus thermarum* or *Zaitzevia thermae* (22). Others are dimorphic with respect to flight wings (37). *Macronychus glabratus*, for example, though often abundant in streams of the eastern United States, is rarely taken in light traps. This is not because it is not attracted to lights, but because only a small percentage of the population possesses functional wings; most individuals are virtually apterous as described by Segal (86). Although Segal depicted *Helichus fastigiatus* and *Promoresia*

(*"Limnius") elegans* with fully developed wings, he made the surprising statement that no species of Dryopidae (including elmids) was known to take flight. Furthermore, having examined over 100 specimens of *Stenelmis crenata* taken at different seasons and sites, and having found all to have vestigial wings, he ascribed this condition to the genus. Actually, *Stenelmis* is our best-represented genus in light-trap collections. Many genera are absent from light-trap collections because the beetles fly during the day rather than at night. It is my impression that most montane elmids are in this category. W. D. Shepard (personal communication) suggests, quite reasonably, that the nocturnal temperatures near most western streams are too low for flight by small insects.

Once they have entered the water, most elmids never again emerge under natural conditions. In fact, they may then be unable to survive out of water for more than a few hours or to successfully reenter the water once they have dried out (111). As yet, very little experimental evidence is available on this point; it may be that some elmids can leave the water and perhaps fly during the first few days or weeks of adult life, and become permanently bound to water as their flight muscles atrophy to provide nutrients for egg production, etc. At any rate, some flying individuals appear to have spent a bit of time underwater. Adults are long-lived, but there are no precise data on specimens under natural conditions. In the laboratory, some individuals survive for several years at room temperature, even under adverse conditions (24, 34).

LARINAE Most members of this subfamily deserve designation as riffle beetles only during the larval stage, when they are completely aquatic and indistinguishable as a group from larval Elminae. Adults of North American genera are riparian, have a relatively short life cycle, and probably enter the water only to oviposit. When disturbed, they fly readily and quickly, sometimes swarming in the spray of waterfalls or cascades. However, adults of some tropical genera normally occur beneath the water surface (22, 25, 101).

Steedman (96) is the only person who has made a detailed study of the life history of a larine elmid. Of *Lara avara,* which inhabits streams of the Coast Range in Oregon, he wrote: "Adults live approximately three weeks, and occur from May to August. Females lay 100–150 eggs on submerged wood. Larvae grow through seven instars, taking about one year for instars 1–3, and from three to six years for instars 4–7. Last-instar larvae leave the water in the spring, and burrow into moss at the edge of the stream. Pupation occurs when the moss dries in early summer. The pupal stage lasts at least two weeks." The larvae feed on decaying wood.

Dryopidae

Adults of *Helichus* occur widely in riffles and are often among the most abundant insects in rivers of the southwestern United States. Of special interest is the fact that *Helichus* larvae are terrestrial rather than aquatic (4, 10, 21, 112), whereas virtually all other aquatic insects are aquatic either only as immatures or as both immatures and adults. *Elmoparnus* inhabits riffles in Central and South America, and may share this unusual developmental feature, but its larva is as yet unknown; adults are less well adapted to aquatic life than are those of *Helichus*, but deserve mention for their peculiar use of antennae in replenishing a ventral air bubble (95). Like the elmids, many dryopids make dispersal flights, and great numbers of some species are taken in light traps. In the eastern United States, *Helichus lithophilus* is the dryopid most commonly collected in light traps.

No complete life history of *Helichus* has yet been published, but G. Ulrich (personal communication) is describing the last-instar larvae and pupae of *H. suturalis* and *H. productus*. He has reported evidence that larval development requires 2–3 yr for *H. suturalis* and 4–5 yr for the larger *H. productus*. Larvae of both species were found in slightly moist sand about 5 m from the stream edge and 2 m above the water level, where they presumably feed upon roots and/or decaying vegetation.

Lutrochidae (Formerly Part of Limnichidae)

Adults of *Lutrochus laticeps* in the eastern United States, *L. arizonicus* in Arizona, and some neotropical species are typically riparian and are capable of flight when disturbed (22, 28). Adults of *L. luteus* in Texas and Oklahoma are more inclined to be aquatic, commonly remaining submerged long enough to acquire heavy calcareous coats. They graze upon travertine-forming algae, mate briefly, and oviposit by inserting their eggs in the travertine, into which the larvae burrow (H. P. Brown, unpublished observations). Pupation occurs in cells above the water line, often within the travertine or rotten logs. Recently eclosed adults are attracted to light while on dispersal flights. In Oklahoma, adults are present from late May through September.

Psephenidae

PSEPHENINAE In the eastern United States, adult males of *Psephenus herricki* are usually noticed as black, soft-bodied beetles approximately the size of houseflies, nervously scurrying over stones that project above the water in stream rapids. When approached, they fly quickly to other rocks and resume their busy search for females. Copulation is brief and has seldom been observed. Mated females crawl down into the water, where they spend the rest of their lives (probably no more than a week or so) seeking suitable sites and ovipositing on the lower surfaces of stones in the riffle. Adults eat little or nothing (1, 75, 110).

The bright yellow eggs, clustered in a mass of up to 600 in a single layer, are familiar to most stream biologists. In Ohio and New York, hatching occurs in 10–15 days and eggs can be found throughout the summer (75, 110). In the tropics, psephenid adults and eggs are present at all times of year, but the adults are rather short-lived and may die before their eggs hatch.

Psephenid larvae (water pennies) are reminiscent of trilobites in form, broadly oval, conspicuously flattened, and often colored so much like the rocks to which they cling that casual observers fail to detect most of them. Because they are present in streams year-round and are frequently abundant, water pennies are probably recognized by more biologists and laymen than any other dryopoids. West (110) observed that they graze during the night and on very overcast days upon the crop of diatoms and other algae covering stones in riffles, and retire to the undersides of the stones during sunny hours. Larvae are inactive during the winter; they do not feed at temperatures below 13°C (75). There are about six larval instars. Mature larvae leave the water during spring or summer of their second year. The larvae do not construct pupal cases in soft, moist soil as stated by White et al (112), nor do they pupate within the last larval skin. Rather, they pupate beneath the carapace of the larval cuticle, which is plastered to the substrate all around by its marginal ciliary fringe. The rest of the larval exuviae forms a wad, also beneath the carapace. Pupation requires about 10–11 days, and occurs on a solid substrate in a moist site beneath or on the side of a rock or log anywhere from a few centimeters to several meters from the water's edge.

In the case of the small tropical and subtropical psephenids, it is possible that the entire life cycle may require less than a year.

EUBRIANACINAE Although it has not been studied in detail, the life history of *Eubrianax* appears to be quite similar to that of *Psephenus*, except that the pupa is not completely beneath the last larval carapace. Instead, the last several abdominal segments of the larval skin are replaced by rather similar ones that belong to the pupa; thus, these tergites of the pupa are exposed, whereas no part of a *Psephenus* pupa is exposed (11, 53). Despite Essig's statement (40), pupation does not occur under water. Clark & Ralston (33) kept 40 larvae in an aerated aquarium; about half of them pupated, in every case on rocks above the water line. I have collected many pupae and eclosing adults, all out of the water and in sites like those where *Psephenus* pupae are found.

PSEPHENOIDINAE (OR PSEPHENOIDIDAE) I have not observed living specimens of the Asian/African genus *Psephenoides*, and no life history study has been published. From Champion (31) we learn that adults and larvae exhibit behavior much like that of *Psephenus:* "[Adults were] Found flying over shallow running water and settling on the partially submerged stones, the females sitting on the undersides of the stones like an Elmid, twenty males seen on one stone, these flying off when approached. . . . Larvae and pupae . . . [are] found in abundance on the submerged stones." Unlike those of *Psephenus*, however, the pupae are aquatic (31, 42, 52, 53, 55), and the adults, at least those of *P. volatilis*, are attracted to light (32). Immatures of an African species, *P. marlieri*, occur on the undersides of submerged rocks on the shore of Lake Tanganyika, much as larvae of the American *Psephenus herricki* live on rocky or gravelly wave-washed shoals in Lake Erie, where I first saw water pennies.

Morphologically, the larvae of *Psephenoides* resemble those of eubriines more closely than they do those of *Psephenus* or *Eubrianax* (13, 53).

EUBRIINAE (OR EUBRIIDAE) Adults of *Eubria* were known in Europe for over a century before the larva was described, and even then it was described as that of a dryopid (64). In fact, most of the eubriine larvae now identifiable to genus were initially considered dryopids because Kellicott (63) described and illustrated a larva he supposed to be *Helichus*, but which was actually *Ectopria*. It was not until 1939 that anyone correctly identified eubriine larvae, when Bertrand reared *Eubria* (9).

Eubriine larvae ("false water pennies") superficially resemble the *Psephenus* larva, and some share its habitat and food. Overwintering occurs in the larval stage. The mature larvae leave the water for pupation, but do not make use of the last larval skin as a tent or shield beneath which to pupate.

Adults are even less like *Psephenus* in behavior. Those of *Ectopria* are nocturnal and attracted to light. They exhibit little interest in water. Nothing is known of mating behavior or oviposition except that both must be different from those of *Psephenus*. In suitable streams of eastern Oklahoma, larvae of the two genera are common and may occupy the same rock; they may also pupate side by side. Then they part company. *Psephenus* males spend the sunny hours on exposed rocks in riffles while females oviposit within the riffles. In contrast, *Ectopria* adults spend their days resting on the lower sides of leaves of trees and shrubs near the stream. I have never seen them on rocks or in the water, nor have I seen any sign of their eggs. At night they become active, but their activities, aside from movement toward light, have not been described. It is surprising that a species as widely distributed and locally abundant as *Ectopria thoracica* in the eastern United States should be so poorly known.

RESPIRATION

Perhaps the most interesting feature of riffle beetles for the average biologist is the underwater respiratory device used by adult elmids and the dryopid *Helichus*. When the beetles first enter the water, they take with them a film of air covering an appreciable portion of their body surface. This thin sheet of air, the plastron, functions as a gill, and is in contact with the air space beneath the elytra, into which the spiracles open. As oxygen is removed from this reservoir by absorption for respiration, it is replaced through diffusion of dissolved oxygen from the surrounding water (2, 15, 44, 45, 104, 105). Existence and maintenance of the plastron is made possible by a dense coating of specialized hydrofuge setae. Scanning electron microscopy reveals remarkable diversity in the microstructure of these setae among elmid genera (56–58). In some genera, such as *Pagelmis* and *Stenhelmoides*, other structures provide a plastron (91). [Some authors have found it convenient to use the term "plastron" to refer to the area on the body occupied by these hydrofuge hairs, scales, etc, as well as to the gas film that is present only when the beetle is immersed (70, 91)]. Some elmids (e.g. *Riolus*) supplement their plastron from oxygen bubbles released by photosynthesizing aquatic plants; others (e.g. *Elmis*) remain permanently submerged without such supplementation as long as the dissolved oxygen level in the surrounding water is adequate (15, 49, 104, 105). Messner & Langer (70) have provided evidence that gaseous exchange between enclosed air spaces of the elytra and the surrounding water may occur directly through thin regions of elytral cuticle.

As one might expect, reliance upon plastron respiration restricts most elmids to waters nearly saturated with dissolved oxygen, hence to typically shallow, fast-flowing, cool, or cold streams. A few enterprising species have succeeded in colonizing other habitats. Probably the easiest transition has been to wave-washed lake shores, as evidenced by *Dubiraphia brunnescens* in California's Clear Lake (22). In shallow midwestern lakes *Stenelmis quadrimaculata*, which does not require wave action, thrives in marl concretions (22, 102). In isolated western localities endemic species of *Microcylloepus, Stenelmis*, and *Zaitzevia* are known from thermal pools and springs. But most remarkable by far is *Austrelmis consors*, which occurs in Lake Titicaca at depths as great as 11 m and in hot springs at temperatures up to 29°C (27, 50). Even in cool, clear, well-aerated streams, other riffle beetles are rarely taken at depths greater than 1–2 m.

Spangler (92) recently described the eyeless genus *Anommatelmis* from wells in Haiti and suggested that its extensive plastron might represent an adaptation to low concentrations of dissolved oxygen. Other genera with comparably extensive plastrons *(Pagelmis, Stenhelmoides)* have been taken only in light traps; perhaps they, too, live in some sort of stagnant habitat that has not yet been sampled (91).

Although adult elmids of the subfamily Larinae lack plastrons and are typically riparian rather than aquatic, the behavior and structure of adults of the African genus *Potamodytes* enable them to remain indefinitely beneath the water surface. I know of no mystery novel more spellbinding than Stride's article (101), in which Bernouilli's principle is shown to play a pivotal role in the formation and maintenance of a large respiratory bubble. Such neotropical genera as *Hispaniolara* and *Potamophilops* apparently use the same strategy (25).

Pollution by soaps and detergents is understandably disastrous to adult elmids because such wetting agents make it impossible for the beetles to maintain either a plastron or a bubble (17). This is a widespread problem in less developed regions where streams are used for bathing and clothes washing. In arid regions the problem is most acute, for such pollution is concentrated at the source of the only available water.

All elmid larvae have basically the same type of respiratory apparatus (39, 49, 71, 80, 102). Tripartite tufts of tracheal gills are extruded from the anus, but can be quickly withdrawn and covered by a hinged operculum. Larvae of *Lutrochus,* Eubriinae, and Psephenoidinae use almost identical mechanisms (3, 49, 68). Larvae of Psepheninae and Eubrianacinae have instead a series of paired non-retractile tracheal gills that arise from the ventral sides of four or five abdominal segments (49, 53).

The pupae of *Psephenoides* are remarkable in that they are aquatic and have tufts of spiracular gills, which arise from the lateral margins of the abdominal segments (13, 49, 52, 53, 55, 68). Some specimens of *Psephenus murvoshi* successfully pupate under water in certain warm springs in Arizona and Chihuahua (76). However, they show no perceptible respiratory adaptations, so the feat seems all the more astonishing; most *Psephenus* pupae and prepupal larvae whose gills have withered simply drown if the rocks to which they are attached are submerged. The respiratory mechanism has not yet been explained. Perhaps in these springs the prepupal larva somehow manages to trap and retain a bubble beneath the carapace that functions like the plastron of adult elmids.

ECOLOGY

Riffle beetles exhibit appropriate adaptations to their particular benthic habitats. Adult elmids that inhabit shifting sand and gravel are commonly plump, compact, and heavily sclerotized (e.g. *Austrolimnius, Elmis, Optioservus,* *Oulimnius*, and *Xenelmis*). If they are dislodged by turbulent water or subjected to abrasion by tumbling sand and pebbles, as must frequently happen, they further minimize injury by retracting vulnerable appendages. Larvae of such genera are also relatively compact and are capable of curling up like armadillos or pillbugs. In contrast, beetles that occupy submerged vegetation or dead wood or that live in slower water tend to have elongated bodies, long legs, and prominent claws (e.g. *Ancyronyx, Dubiraphia, Hintonelmis*, and *Macronychus*). Collecting techniques such as kick-sampling or Surber sampling are very effective for the former group, but useless for the latter.

Because of their depressed onisciform structure, which makes boundary layer control possible (89), water pennies and their ilk require a solid and relatively level substrate to which they can cling, preferably rocks.

Larvae of *Lutrochus* and the elmid *Hexacylloepus* tunnel in the porous travertine of southwestern streams, presumably deriving their nourishment from the embedded algae. Most elmid larvae ingest algae and debris with less crunchy roughage. Xylophagous larvae such as *Lara* and *Macronychus* chew their own grooves in sunken wood, probably gaining most nutrition from the fungi and bacteria responsible for the decay of the wood (41, 96). The great quantities of frass they generate indicate that only a small proportion of their ingested food is digestible. It is conceivable that the caeca at the anterior end of the midgut of most adult elmids (1, 51) harbor symbiotic microorganisms that aid in digestion; however, no evidence has been adduced for this, and the caeca of xylophagous beetles are no more prominent than those of beetles that feed on algae and detritus.

Feeding ecology varies among species, and even more among genera (67, 85). Judging chiefly from gut contents, it appears that most riffle beetles, both as larvae and as adults, subsist on microorganisms and debris scraped from the substrate. The siliceous tests of diatoms are often the only recognizable items in the gut, but they are gratifyingly identifiable (43, 67, 85).

Steffan (97) showed in central Europe that the largest species within any genus inhabits the zone of least temperature fluctuation, and that cold stenothermic species are always bigger than eurythermic species. No comparable study has been made in the New World, but the principles seem to apply only in selected genera, e.g. *Heterelmis*.

Turcotte & Harper (106) found that in a small Andean stream the density of elmids was largely regulated by spates. This may be the case in many nonseasonal streams subject to spates.

Several authors have mentioned apparent gregariousness. The suggestion is understandable. I have counted 29 *Ectopria* larvae on a fist-sized rock, and both larvae and pupae of *Psephenus* sometimes seem crowded on a stone. Dozens of male *Psephenus* may be seen on a projecting rock in stream rapids, and scores of *Lutrochus* adults may be squeezed into streamside crevices.

Nevertheless, such aggregations are probably attributable to the microenvironment rather than to true gregariousness; a combination of factors makes the favored spot the most logical and suitable site for any of the individuals to find and settle upon. The popular spot never seems an inappropriate one, and usually can be seen to be the most favorable. In other words, I think that the probability that each individual would have found that rock or crevice is independent of the presence, absence, or proximity of other individuals. This hypothesis should be amenable to experimental investigation.

During my early years as a riffle beetle enthusiast (23) I assumed that elmids and perhaps other riffle beetles required permanent streams, and that no obviously temporary stream was worth checking. How many interesting specimens I missed for this reason I shall never know, but in arid and semiarid regions the loss was greatest. Then I noted that water pennies clinging to boulders could crawl down the rock surface into the sand to remain beneath the level of the water as it receded into the sandy/pebbly substrate when the stream bed appeared to have dried up completely. By digging into damp sand, especially sand in contact with large stones, I found that the last part of a riffle to dry up could be a profitable collecting site. A dried-up creek near Waxahatchee, Texas yielded a total of 285 adult and 173 larval *Stenelmis*, 2 adult *Heterelmis*, and 1 *Helichus*. Bell (5) found *Narpus* and *Zaitzevia* adults in moving water 40–50 cm beneath the gravelly surface of a dry stream bed in California. Some of my best collecting in Baja California has been in such stream beds, especially where an occasional trickle has suggested recent surface flow.

A few pragmatic biologists have capitalized upon the fact that many riffle beetles (and other creatures) are finicky about their choice of habitats, and have devised a means of evaluating the water quality of streams by sampling and scoring the dryopoid fauna (47, 88, 108). At times I find it handy to be able to cite such potentially utilitarian aspects of the work I do.

RELATIONS WITH OTHER ORGANISMS

Predators

As far as we know, predators have but a minor role in the affairs of riffle beetles. I know of only one report that contains pertinent data, that of Stewart et al (99) concerning food habits of hellgrammites, larvae of the megalopteran *Corydalus cornutus*. Three elmid genera were among the prey: *Dubiraphia*, *Heterelmis*, and *Stenelmis*. However, it appears that hellgrammites did not find the elmids exactly delectable, for elmids represented only 0–1.6% of the organisms found in the predator guts, whereas these elmids represented 3–12% of the organisms available as potential food.

The coloration of many adult riffle beetles is quite conspicuous. Some, such as *Macronychus*, are jet-black and shiny, with contrasting silvery-white areas covered by the air film of the plastron. Others, e.g. *Optioservus*, *Promoresia*, *Gonielmis*, and *Dubiraphia*, are black with colorful spots or streaks of yellow, orange, or red on their elytra. In *Ampumixis*, *Heterlimnius*, and *Narpus* the bright colors form broad transverse bands, and in *Ancyronyx* they produce eye-catching loops. It seems reasonable to surmise that the possessors of such presumably aposematic pigments and patterns would probably be unpalatable to predators. D. S. White (personal communication) has tested this hypothesis. He found that none of the tested elmids were acceptable as food to any of various predators that share the habitats of local elmids (e.g. crayfish, turtles, sunfish, and darters), although the predators readily consumed other prey organisms of comparable dimensions. When the predators accidentally ingested elmids with other food, they typically spit them out. The beetles apparently possess some sort of chemical defense that repels diverse types of potential predators. This line of investigation should be interesting to pursue.

Homo sapiens is the only species I know of that has developed a taste for riffle beetles. Over a century ago Philippi (81) described a new species of elmid from Peru, which he named *Elmis condimentarius*. The generic name was shifted to *Cylloepus*, then to *Macrelmis*, and finally to *Austrelmis* (27), but it is the specific epithet, *condimentarius*, that suggests the species' distinction. I take the liberty of presenting my free translation of the first few sentences of Philippi's intriguing paper:

> A short time ago I received from Dr. Barranca in Lima some insects in a paper package, and in a bit of paper a clump of small beetles with the following note: "Insects that people form into lumps of paste known here under the term chiche; they serve as seasoning for food which they call chupe de chiche. They are found in the quiet waters of brooks and streams of the mountains, and their commercial value is not inconsiderable."
>
> Concerning the taste of the beetles I cannot say anything, for I promptly threw them into alcohol before I noticed the note. At least 90% of the mass consisted of little beetles like *Elmis* that were well preserved, so that I could extract a couple of hundred specimens and am in the position to provide almost all fellow coleopterists with specimens for their collections, if not for their palates . . .

Had I read Philippi's paper before my 1971 trip to South America, I might have been able to say something about the taste of chiche and whether it is still an item of commerce in Lima. Before I read his paper, all the specimens of *Austrelmis* that I had collected in the vicinity of Lima and elsewhere had long been in alcohol. Perhaps they were once piquant and flavorful, but I can attest that they now do little to titillate the taste buds.

I suspect that riffle beetle larvae are appreciably more palatable to predators than are the adults, but are less readily detected. Larvae dislodged by disturbance of the substrate are devoured by fishes. In streams of the western United States, Mexico, Central America, and the Andean portions of South

America, there are almost always abundant predatory benthic bugs (chiefly naucorids, and perhaps helotrephids in the Andes). These probably include elmid larvae among their prey. Triclad planarian worms, which are often very abundant, are also likely to take their toll on larval elmids and psephenids.

Predation upon elmid eggs would be quite difficult to study under natural conditions, but psephenids provide an ideal setup for both predator and investigator. The gluttonous worms *Dugesia* spp. snuggle right beside ovipositing *Psephenus* spp. with their proboscides extending beneath or alongside the beetles, and ingest the colorful contents of the eggs. The scent of ruptured eggs probably entices other predators and scavengers. I have even seen *Psephenus* larvae and *Stenelmis* adults eat such planarian-damaged eggs, but this could hardly be considered cannibalism.

My report of cannibalism by a larva of *Microcylloepus* (29), which attacked first an adult of its own species and then a fellow larva, probably described aberrant behavior; however, nutritionally deprived individuals perhaps exhibit such tendencies more frequently than we suspect.

Parasites

HYMENOPTERA In 1863, Perez described the parasitic behavior of the tiny hymenopteran *Pteromalus macronychivorus* on pupae of the elmid *Macronychus quadrituberculatus* in France (80). Although he did not make a complete life-history study of the parasite, he succeeded in rearing larvae to pupae and one pupa to an adult female. It might seem surprising that no one else has discovered other such parasites on elmids during the dozen decades since Perez's publication, but very few elmid pupae have been observed under natural conditions. Enterprising investigators are likely to observe additional hymenopteran parasites or parasitoids.

Psephenid pupae are much larger and easier to find than elmid pupae, and are often present in considerable numbers. Two very different species of wasps parasitize pupae and prepupal larvae of *Psephenus* (18, 19). *Psephenivorus*, a eulophid chalcidoid, is so tiny that as many as 39 wasps may develop within a single water penny. Only one individual of the larger wasp *Trichopria*, a diapriid proctotrupoid, develops within a water penny. But parasitism by either wasp is invariably fatal to the host, and the incidence of parasitism may exceed 90% of the water penny population. Thus far, these wasps have not been reported north of the Rio Grande valley.

ACARINA I know of no published studies concerning water mites on riffle beetles, and I presume that they are of little importance. I have found a few attached to adult elmids in Costa Rica, Venezuela, the Dominican Republic, and Brazil. I have also encountered what I took to be eggs of Hydracarina attached to adults of *Microcylloepus* in Texas and *Oulimnius* in Tennessee.

MISCELLANEOUS ARTHROPODS I have noted hemipteran eggs (Corixidae?) on the dorsum of a *Psephenus* larva in Mexico, and dipterous larvae (Chironomidae) on six larvae of the elmid *Potamophilops* in Brazil.

FUNGI Members of the primitive ascomycete order Laboulbeniales are obligate but benign ectoparasites of arthropods. Of 116 genera, 90 are known only from beetles and 9 others parasitize both beetles and other arthropods (6). Although 14 genera occur on other water beetles, only two are known from dryopoids: *Helodiomyces* on *Dryops* and *Cantharomyces* on the dryopids *Dryops, Helichus,* and *Pelonomus,* on *Lutrochus,* and on the larine elmid *Phanocerus* (6, 103; R. K. Benjamin, personal communication). Of these beetles, all but *Helichus* are riparian.

PROTOZOA The organisms most commonly noticed on riffle beetles are attached peritrich ciliates, which are often abundant. Since the ciliate fauna of hydrophilids is quite diverse (69), that of riffle beetles merits investigation. Possibly more exciting are the sessile suctorians that find elmids prime substrates for attachment (98).

A group of internal parasites that deserves mention is the gregarine sporozoans, whose opaque whitish trophozoites and gametocysts are often big enough to be seen through the body wall of dryopoid larvae under low magnification or even with the naked eye. They probably represent undescribed species and perhaps new genera. These sporozoans occur in both adults and larvae (1, 43), but dissection or sectioning is required to observe those in adults. They seem to do little harm to their hosts.

OTHER PROTISTA Diatoms are frequently attached to the cuticle of adult elmids, and filamentous bacteria may render the beetles hairy-looking.

ANCESTRY

The paleontological record provides as yet but little bearing on the ancestry of modern riffle beetles. Material from glacial and postglacial deposits represents a fauna very like that of today (72, 73). A fossil of "*Psephenus*" from the Miocene (83) is not a psephenid or even a member of the superfamily Dryopoidea. In Crowson's opinion (35) the earliest fossil dryopoid is from the Upper Jurassic. He dates the origin of the superfamily from the Lower Jurassic (36) or, if we accept his earlier estimate (35), the late Triassic—about 190 million years ago. His phylogeny is based upon Hennig's principles (46).

The most convincing evidence for the antiquity of riffle beetles lies in the geographic distribution of extant forms, interpreted according to present understanding of plate tectonics and continental drift. Long before the concept of continental drift was accepted, Hinton (48) described a new species of the flightless dryopid *Protoparnus* from the West Indies, pointed out that all previously known members of the genus inhabited New Zealand, and reasoned that there must have once existed land connections between the two regions. The presence of the elmid *Hydora* in South America as well as in Australia and New Zealand supports this interpretation (94). The elmid genus *Austrolimnius,* however, provides the most striking evidence. Of the 78 species now known, 60 occur in Australia and New Guinea, and 18 in South and Central America (26, 54, 56, 57, 61). Some of those in Australia are much more closely related to certain South American species than to any of their fellow Australian species. Thus, if it is true that these continents have been separated since the Lower Cretaceous, such genera as *Austrolimnius* must have been well differentiated at least that long ago.

Presumably the elmid genera *Oulimnius, Macronychus,* and *Stenelmis* similarly antedate the separation of Europe from North America, since they are found in Europe and eastern North America, but not in far western North America, Central America, or South America (26).

The dryopids *Dryops* and *Helichus* are prominent on all continents except Australia and Antarctica (26). Perhaps these genera, like placental mammals, are absent in Australia because they did not evolve until after the separation of Australia from South America, whereas the dryopid genus *Protoparnus,* as mentioned above, is enough older to have been around before those continents drifted apart.

Only three genera of aquatic dryopoids have been reported from both Africa and South America: *Dryops, Helichus,* and the psephenid *Eubrianax* (26). Whether any of these provide strong evidence for migration across the land bridge connecting these continents during much of the Cretaceous is debatable, since all three also occur in North America and Eurasia. Interestingly, no elmids are included in this list. Investigation should surely reveal at least sister groups of elmids in Africa and South America.

SUMMARY

For purposes of this article, "riffle beetles" include the following groups of nonswimming dryopoid beetles that typically occur in shallow, fast-flowing water: all Elmidae and Psephenidae *(sensu lato),* the dryopids *Helichus* and *Elmoparnus,* and the genus *Lutrochus* (Lutrochidae or Limnichidae).

Members of the elmid subfamily Elminae are aquatic as both larvae and adults, and feed chiefly upon algae and detritus scraped from the substrate. Larvae have tracheal gills that are retractable into the rectum. Both larvae and adults are benthic in or on various substrates, but in many species both are capable of controlling their specific gravity and may be taken in drift samples.

In mature larvae of many species, tracheal air sacs provide buoyancy, and drifting assists the larvae in reaching pupation sites. Pupation occurs in a pupal cell in a protected site outside the water. Recently eclosed adults commonly make dispersal flights (often at night) before they enter the water. Some species of elmids lack functional flight wings; others are dimorphic, with alate forms comprising only a fraction of the population. After they enter the water their flight muscles probably atrophy, precluding subsequent flights, and the beetles remain underwater for the rest of their lives, which may be more than a year. They respire by means of a plastron, a film of air that functions as a gill. Mating and oviposition take place underwater.

Members of the elmid subfamily Larinae differ from Elminae in that adults are less long-lived, lack a plastron, and are commonly riparian. Adults of certain tropical genera are aquatic, but have evolved a different respiratory technique employing a large bubble. Larvae of the two subfamilies are essentially alike, but adult ecology and behavior are very different. Adult larines are quite agile; they fly readily and rapidly, in contrast with the slow and water-bound Elminae.

Psephenid larvae are flattened and aquatic, and possess tracheal gills. Members of the subfamilies Psepheninae and Eubrianacinae are quite similar. Their larvae, the true water pennies, exhibit a series of paired, ventral, abdominal, nonretractile gills. By day they cling to the undersides of stones, moving at night to the upper surfaces of the stones to graze upon the algae. They pupate beneath the carapace of the last larval skin, usually in protected sites not far from the water. Adults are short-lived; the males are diurnal, riparian, and fast-flying. After mating, females crawl down into the water and spend the rest of their lives at the task of oviposition.

Larvae of the Eubriinae and Psephenoidinae have retractile anal gills like those of elmids. Eubriines pupate out of the water, but not beneath a larval carapace; adults are nocturnal and commonly spend the day on foliage. *Psephenoides* pupates underwater on the stones inhabited by the larvae; the pupa respires by means of filamentous spiracular gills; adult behavior is apparently similar to that of *Psephenus*.

Adults of *Helichus* behave much like those of elmines except that females presumably leave the water to deposit their eggs in the larval habitat, e.g. sand or soil. No known dryopid larvae live in stream riffles; most are terrestrial. *Lutrochus* larvae are aquatic and resemble those of elmids. The adults are riparian or in some cases aquatic. No complete life history study has been published for either *Helichus* or *Lutrochus*.

Predators seem to pose little hazard to adult elmids, but eggs and larvae are more vulnerable. Lethal parasitic wasps include a pteromalid that attacks pupae of the elmid *Macronychus* in France and a eulophid and a diapriid that attack *Psephenus* pupae and prepupal larvae in Mexico and southern Texas.

Nonlethal parasites include Hydracarina, fungi (Laboulbeniales), and gregarine sporozoans; other protists commonly attached to riffle beetles are peritrich ciliates, suctorians, and diatoms.

Modern concepts of plate tectonics and continental drift not only explain how closely related species happen to occur in regions as widely-separated as Australia and South America, but also emphasize the antiquity of the group.

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