

Thoughts on Aquatic Insects

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Aquatic adults seldom have terrestrial juveniles. Respiratory problems may lead to tropical species being smaller than related temperate ones. Suctorial feeding on higher plants seems unknown. Cryptic coloration is common, aposematic, and epigamic rare. Flightlessness is common, but potentially flying forms must be generally available; this restricts tracheal gills to juveniles. (Accepted for publication 12 January 1981)

KINDS OF LIFE HISTORY

Among the insects of inland waters there are certain peculiar situations which, though often obvious, at first seem hard to explain.

We may group the animals under consideration according to whether they are terrestrial or aquatic in active immature and predominantly trophic stages or in the mature and primarily reproductive climax of their lives. The following matrix shows the orders of magnitude of the four possible classes:

	Adult terrestrial	Adult aquatic
Immature terrestrial	n. 10^5	n. 10^2
Immature aquatic	n. 10^4	n. 10^3

This reveals the fact that it is easier to be immature in the water than to be mature. The category of the aquatic mature stage that has grown up terrestrially is curious-

ly rare, being exemplified only by certain beetles of the families Hydraenidae and Dryopidae (Hinton 1955). Moreover, though the aquatic bugs and beetles together include almost all the members of the adult aquatic and immature aquatic categories, the two orders differ in their relation to water: The endopterygote Coleoptera have a pupa that is nearly always formally terrestrial. It lies in a dry cocoon in a cavity excavated above water-level in the bank of the water; the larva lived in it, and all being well, the adult may return to it.

RESPIRATION IN AQUATIC HABITATS

For a member of a terrestrial group entering freshwater, respiration probably poses a greater problem than does any other vital function. Small aquatic insects (and other animals less than about 1 mm in diameter) are apt to breathe by diffusion over the entire thin, but largely unmodified, body wall. There may be specialized hemolymph sinuses below this wall. When the insect is a relatively long and thin cylinder, one may regard the whole body as a gill.

Many variations on this general theme are found in the Diptera, which commonly have blood gills or special diverticula of the body wall containing sinuses. In many cases, however, these have now been shown to be organs taking up chloride ions rather than oxygen. In some chironomids, the hemolymph contains hemoglobin. Comparable respiration involving the whole surface is common in

the first one or two nymphal instars of many aquatic insects such as the mayflies, the Hemiptera, and the aquatic moth *Acentropus*, though later these develop other respiratory mechanisms. The unique pair of genera, *Idiocoris* and *Paskia*, the smallest of all known aquatic Hemiptera, are apparently the only free-living adult apneustic insects; they are limited to the stony littoral of Lake Tanganyika (Esaki and China 1927).

The large aquatic insects breathe either by tracheal gills, outgrowths of the body wall that are richly supplied with trachea, or spiracles that may be fed from bubbles and replaced periodically by visits to the surface or to photosynthesizing plants. Such bubbles or air-stores are held in various ways. Immature insects retain air-stores usually in bunches of hair; in mature insects, the elytra of beetles or the equivalent hemelytra of bugs cover a large dorsal air-store. There may also be very fine hairs carrying air on the surfaces of various parts of the body, which give the insect its "silvery-light" appearance, as Mary Ball (Ball 1846) called it 140 years ago. From the air-stores, air is usually passed into the tracheal system much as in terrestrial insects.

Since the air in the air-store is in contact with water, it can act as a "physical gill"—a universal, though rather odd, appellation (Ege 1915, Popham 1964, Thorpe 1950). As respiration takes place, oxygen is removed; the equivalent carbon dioxide produced is much more soluble than the oxygen and quickly passes into the water, so that the bubble constituting the air-store contracts. The partial pressure of nitrogen in the bubble therefore increases, so nitrogen diffuses out. Since oxygen is lost by respiration, the partial pressure of that gas decreases, and oxygen diffuses into the bubble, at least from saturated water.

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Ideally, the process can continue until all the nitrogen has been lost; but in actual cases, as the bubble becomes small, the oxygen content becomes dangerously low, and the air-store must be replaced at the surface, well before it disappears. The effectiveness of the process depends on the oxygen concentration in the water, which is related inversely to the temperature. It also depends on the exposed surface of the bubble, which, in a large animal, is smaller relative to the mass of metabolizing tissue than in a small one. Thus, the physical gill works best for small animals at low temperatures, but the effectiveness varies greatly with the morphology and physiology of the organism under study. Under favorable circumstances, the mechanism of the physical gill can certainly increase severalfold the period between surfacing, thereby reducing the risk of predation.

High temperatures not only decrease the physical gill's effectiveness, but also increase the metabolic demand for oxygen. Very little, unfortunately, is known about respiration in tropical aquatic insects, though Miller (1964) has clear evidence that the physical gill can work for *Enithares sobria* Stål, a backswimmer widespread in Central Africa. In the Corixidae, the larger Corixinae are predominantly temperate with a maximum number of species in the United States, whereas the smaller Micronectinae are largely tropical with the richest local fauna in Sri Lanka. In tropical uplands, such as the Nilgiri Hills in India and the mountains of Ethiopia, Micronectinae, as in temperate regions, tend to be rarer than Corixinae. These features of the distributions of the Corixidae are, thus, in line with small species being better adapted to warm climates, perhaps because they have greater ease in breathing.

Two remarkable respiratory specializations are known in particular groups of submerged insects. A few species of naucorid bugs and elminthid beetles have evolved an extreme development to the physical gill. A large area of the body is covered with a pile of very fine short hydrophobe hairs. In the Palaearctic naucorid *Aphelocheirus*, there may be 2.5 million such hairs (about 6 μ long) per mm² (Thorpe 1950). At ordinary subaqueous pressures, surface forces prevent water from penetrating the pile, which remains the support for a thin dry gaseous layer, acting as a physical gill, from which specialized spiracles can receive air.

The insects that have perfected this respiratory plastron live in habitats where continual disturbance, or the photosynthetic activity of calcicole algae, keeps the water saturated with oxygen. Though in a perfectly developed case, such as that of *Aphelocheirus*, the plastron obviates the necessity for surfacing, it is evidently not a mechanism that can be effective in a wide variety of habitats.

A second specialization of the air-store is found in the lesser backswimmers of the subfamily Anisopinae in the family Notonectidae: the genera *Anisops* living in the warm temperate and tropical Old World and *Buenoa* in the New. These insects have an abdominal hemoglobin organ, richly supplied with tracheae. The hemoglobin in the cytoplasm of the cells of the organ is charged with oxygen at surfacing and slowly liberates the gas as it is used in respiration. The insect thus can adjust its density, remaining poised at the same depth for some minutes (Miller 1964).

Most adult insects living on the bottom or among weeds, if they use an air-store for respiration, will have to make frequent visits to the surface, except perhaps when dormant in winter. Such expeditions are energetically wasteful and limit the depths that can be colonized. Moreover, surfacing is bound to be a conspicuous act, increasing the dangers of predation. In spite of these disadvantages, no adult aquatic insect respire by tracheal gills, though such structures are obviously highly successful in the physiology of mayfly and stonefly nymphs and in more elaborate ways in those of dragonflies and damselflies, in the larvae of alderflies and caddisflies, and in those of some beetles and two-winged flies.

A TREND TO SELECTIVE OMNIVORY

The feeding habits of aquatic insects are much more varied than their modes of respiration. Usable energy and the elements required in nutrition, other than hydrogen and oxygen, are obtained from many sources in a variety of ways.

The earliest putative aquatic insects, the Protodonata, were presumably carnivores, as are their immediate successors, the Odonata. The largest Protodonata, giants with a wingspan of up to 75 cm, must have had proportionately large nymphs of great repacity, which probably took a number of years to reach maturity. In their late instars, they may well have eaten fishes.

The oldest mayfly nymph of which the mouth parts are known in detail is *Kuka-*

lova americana Desmoulins from the Lower Permian of Oklahoma. Because the mandibles were very large and bore teeth, Kukalová (1968) initially regarded the insect as a carnivore. Later, Hubbard and Kukalová-Peck (1979) compared the mouth parts with some modern generalist feeders. Though the evidence is still inadequate, it seems that the mayflies may exemplify a trend detectible in other freshwater invertebrates that have evolved a kind of selective omnivory. For such animals, the haptobenthic algae and bacteria with the slime secreted by them, together with adherent detritus and associated small animals, constitute a universal pabulum covering all surfaces, at least in the shallower parts of temperate freshwaters (except perhaps the most oligotrophic). A change from carnivory to partial reliance on such a source of food, together with any other plant or animal matter that may be available, seems to characterize many of the small Corixidae and some species of Haliplidae.

Development of a like kind of omnivory is known in the Lymnaeidae among the watersnails. In all cases, some degree of selectivity is retained, though the range over which it is exercised is greatly extended. Some animals eat most algae other than *Cladophora*, or most angiosperms other than *Elodea*. These two plants are apparently largely inedible (and so most successful). The former is apparently protected by lauric, myristic, and palmitoleic acids (Lalonde et al. 1979, Larson 1981), which render the plant poisonous, or at least inhibitory in various ways to mosquito larvae, gastropod mollusks, and crayfish.¹ Unfortunately, except for *Nuphar* and *Nelumbo* (which are full of strange alkaloids), little is known of secondary compounds of a defensive kind in freshwater vascular plants. The existing data (or lack of it) suggest that such compounds are of less significance than on land, but this well may be an illusion based on ignorance. Even the most inedible plant will ultimately add to the food reserves, producing, when it dies, detritus and nutrients for algae and bacteria.

Generally, almost any moving food may be pursued by predatory aquatic insects, though the size and ease of handling make a great difference to what is actually taken. There are very few cases of food being rejected: *Notonecta undu-*

¹Ruth Patrick, School of Forestry and Environmental Studies, Yale University, personal communication, November 1980.

lata Say refused a pink phyllopod of uncertain identity; *N. uhleri* Kirkaldy will not eat *Buenoa*; and a few of the Belostomatidae are specialized as predators on gastropod snails.

Most waterbugs are still suctional carnivores; this is probably true of many corixids, even though others feed on haptobenthos. Indeed, fully aquatic insects have not developed the habit of sucking the fluid contents from vascular waterplants, though corixids and some larval haliplids may suck out all the contents of the cells of filamentous algae. There are no freshwater analogues to the vast array of Myridae in the Heteroptera, nor to the whole of the Homoptera. In the latter suborder, a few aphids are found on the aerial parts of emergent waterplants, but not under water. The absence of aquatic insects that suck higher plants may be of great antiquity. The Paleoptera, the more primitive group of flying insects, seems to have consisted in the late Palaeozoic of mandibulate orders with aquatic nymphs, which survive as mayflies and dragonflies, and extinct terrestrial haustorial orders (Palaeodictyoptera, Megasecoptera, and Diaphanopterodea), the sucking mouthparts of which are apparently derived from mayfly-like trophi (Hubbard and Kukalová-Peck 1979, Kukalová-Peck 1978).

CRYPTIC COLOR AND CHEMICAL DEFENSES

Aquatic insects are, of course, themselves subject to predation. Macan (1966) particularly has shown how important the littoral vegetation can be in determining if such insects can coexist with fish. The matter is clearly very complicated, depending largely on the species of predator and prey as well as the nature of the protective environment.

Striking reactions to predation have evolved. Popham (1941) found that most corixids tend to match the albedo of their background. The process is ontogenetic, depending on the background to which the insect is exposed three days before a moult. The corixids are so imprinted on the background that they become restless when placed on one that they do not match, even though they probably have no way—because of the geometry of their eyes and dorsal surfaces—of directly comparing their own coloration with that of the background on which they are perching. If, after a migratory flight, they enter a body of water with an inappropri-

ately colored bottom, they leave. Both in the laboratory and in nature, the matching can be shown to be effective against predation (Popham 1942, 1944).

A similar tendency to match a light or dark background occurs in some waterbeetles, notably the Haliplidae.² However, in holometabolous insects, which may have different larval and adult habitats, the variation in the adults is probably determined genetically rather than environmentally.

Many beetles secrete toxic secondary compounds in their pygidial or thoracic glands (Miller and Mumma 1976, Schildknecht 1970). In the Dytiscidae, at least in the subfamilies containing the larger species (Dytiscinae and Colymbetinae), the thoracic glands produce an astonishing array of steroids related to or identical with mammalian sex hormones. These are repellent, anaesthetic, or, in sufficient dosage, lethal to fish. In the Gyrinidae, norsesquiterpenes, produced in the pygidial glands, act similarly. The other families of waterbeetles have not been adequately studied, and the waterbugs, as well as the beetles, produce odors that may be repellent, but relatively little work has been done on their chemistry.

BREEDING, ASYMMETRY, AND SONG

There are certain very peculiar specializations related to reproduction. For the most part, they do not yet fit in with the other aspects of the life of insects underwater to make a unified story. Hungerford (1919) indicates that the male of *Notonecta irrorata* Uhler habitually takes up a position to the left of the female in mating, even though his exoskeleton and genitalia are not asymmetrical. In some naucorids, notably the common European *Ilyocoris cimicoides* (Linnaeus), the muscles of the male abdomen are asymmetrical, even though the exoskeleton is not. In some tropical members of the family (*Macrocoris*, *Neomacrocoris*), the seventh tergite of the male has asymmetrical lobes on its posterior margin, but their function is unknown. The Anisopinae have asymmetrical parameres or claspers, though the rest of the abdominal bodywall appears symmetrical. In the Corixidae, the whole of the abdominal exoskeleton from the fifth tergite backwards is extremely asymmetrical.

²E. J. Pearce, personal communication.

In most Corixidae, the male bears on the right side of the sixth abdominal tergite a condensed group of spines, usually forming several regular rows, called the strigil. In the very primitive Australian *Diaprepocoris*, the strigil is double, as if the left member of a pair of lobes had moved across the body to engage with the right, perhaps making a sound-producing organ. In the small and largely tropical Micronectinae, the strigil is developed as a row of short, wide spines on the right of the sixth abdominal tergite of the male. It is certainly a sound-producing organ, plucked by a plectrum formed from the right posterior margin of the fifth tergite (King 1976).

In the Corixinae, a well-developed strigil is present in most species. Mary Ball (Ball 1846), who first heard Corixidae stridulate in 1840, recorded abdominal movements, as in *Micronecta*, accompanying one type of sound made by *Sigara dorsalis* (Leach). No one else has seen any part other than the anterior legs being moved in relation to sound production in the Corixinae. In this subfamily, the strigil is probably used to increase the grip of the male on the female during coitus, though in many cases the structure looks like a sound-producing organ. In the Corixinae, the known stridulatory structures are a patch of short, pointed spines forming a *pars stridens* on the anterior femur of the males of many and the females of a few species, and a *plectrum*, a ridge on the edge of the head on which the *pars stridens* is rubbed (Jansson 1972). The sounds are mainly used in courtship, but they also may be employed to achieve a certain degree of spacing between males in a sort of territorial arrangement. Very remarkable differences in behavior on the part of closely allied species have been recorded by Jansson (1979); the comportment of the male of *Arctocoris germari* (Fieber), which always waits for a reply from the female he is courting, contrasts with the activity of *A. carinata* (Sahlberg), which often engages in rape (Jansson 1979).

Though in most genera the strigil lies on the right side of the sixth abdominal tergite, throughout the family occasional sinistral specimens are recorded in a number of species. A few are regularly dimorphic, and others (*Corixa*, *Trichocorixa*, *Heliocoris*) practically always have the strigil on the left. When this inversion occurs, it affects only the muscles and exoskeleton of the abdomen; other asymmetries remain unchanged. In one of the dimorphic species, *Ahuautlea mexicana* de la Llave, the homozygous

sinistral is lethal (Peters 1960). (There must be intense selection of heterozygotes bearing the sinistral gene.)

Very elaborate sound-producing mechanisms used in courtship are also found in the small backswimmers of the subfamily Anisopinae: *Anisops* in the Old World, *Buenoa* in the New. The few of the 175 species that have been studied differ markedly in the details of their behavior. The Anisopinae use a tibial comb on the anterior leg against a pair of prong projections for the beak as their main vocal organs; as well as sound, a characteristic pattern of movement varying from species to species is involved in courtship (Goertz 1963, Wilcox 1975).

Sound production is also recorded but hardly studied in a few other waterbugs and waterbeetles. Where it is used in an elaborate way in courtship, as in the Corixidae and Anisopinae, it seems characteristic of rather gregarious species ordinarily exhibiting little intraspecific aggression, unlike the potentially cannibalistic and very well-spaced Notonectini. This needs further study, as does the possibility that underwater auditory stimuli are better epigamic signals than are visual ones. Of course, they may be dangerous if there are predators around with receptor organs for sound. As in fishes (Popper and Coombes 1980), pitch plays little or no part in communication, which is primarily based on the length and spacing of trains of pulses.

FLIGHT AND FLIGHTLESSNESS

Finally, there is a systematic difference between the flightless forms of terrestrial bugs, usually apterous with vestigial elytra, and the flightless waterbugs and waterbeetles, in which the hemelytra or elytra are almost always large enough to cover a significant dorsal air-store. Only when there is a respiratory plastron, as in *Aphelocheirus*, does a condition develop comparable to what is found on land.

Very often in those Corixinae in which neither hemelytra nor wings are reduced, the insect is flightless because the indirect flight muscles that normally fill the thorax fail to develop at the last moult (Young 1965). This failure is usually temperature-dependent; only over about 15° C does the adult insect emerge as a flying form (Scudder 1976, Scudder and Meredith 1972). In the Micronectinae of temperate countries, nearly all specimens are flightless, about 2% having fully developed wings. The nature of the determination is unknown, though the

existence of the rare flying forms is important in dispersal (Wróblewski 1958). In *Micronecta* in tropical lands, many species are always—and most are frequently—winged, suggesting that in areas in which shallow water frequently dries up, flight is an essential function.

Flightless Corixidae with undeveloped muscles live longer and are more fertile under suboptimal, but not under optimal conditions, than fully developed specimens. When conditions are poor, the economy of not having to support the basal metabolism of a thorax full of flight musculature evidently better adapts the flightless forms, except that they are unable to fly away (Young 1965).

Less is known about the pterygodimorphism of beetles (Jackson 1956) than of bugs, but there is some evidence that the condition is genetic (Angus 1970).

THE DANGERS OF BEING TOO AQUATIC

In transient environments, which nearly all bodies of freshwater ultimately are, some opportunity for dispersal is necessary for the continued existence of a species. The nearer that this opportunity is to the reproductive phase in the life history, the more effective it will be. For any generation, the population will be greatest when present as newly fertilized eggs before any mortality has occurred and with the maximal chance of at least a few individuals being delivered into some unusually favorable environment. Since, to a flying insect, the period of flight is also the period of maximum potential dispersal, aeroterrestrial life would be expected at the time of reproduction. This would explain the rarity of species with terrestrial larvae and aquatic adults.

The absence of any adult insects with tracheal gills at first seems peculiar because any kind of respiration involving surfacing is always wasteful and necessitates the use of energy in moving to or from feeding grounds to the surface. The range of depths that can be occupied is clearly limited; nearly all waterbugs and waterbeetles never descend below a few meters. Moreover, surfacing is a dangerous activity not only to insects in torrential waters for mechanical reasons, as Parsons (1974) has pointed out, but also because, by making insects move conspicuously, it makes them more available to predators.

An enormous number of immature insects of all sorts of shapes, sizes, and

textures have tracheal gills. Why, when such organs would seem advantageous, do no adults? Perhaps, if an insect is to have gills, it must either give up flight or develop some mechanism for keeping the gills moist on land and in the air. Land crabs can do this, walking even on dry coral islands, as the branchial cavity provides a way to keep the gills moist. But there is no obvious preadaptation that would permit the development of such a shield in either order containing adult aquatic insects. Though many species of aquatic insects do not fly, very little genetic or environmental change would probably be needed to convert almost any actual nonflying species into one that can fly. Whatever may cause the appearance of fully developed macropterous forms in up to about 2% of the population of the Palaearctic species of *Micronecta*, the chance of any individual being able to fly is small. But the chance of there being some individuals, in a drying habitat, that could fly away to a more permanent body of water is great. Wróblewski (1958) has given actual examples that indicate that such behavior would be quite possible in nature. In an extreme case of genetically determined wing development, back-mutation might be successfully balanced against the selection in favor of a flightless form. This would permit survival of the species so long as aerial respiration remained possible. If tracheal gills had been evolved, the species might be completely unable to look for new habitats as the water dried up. Thus, the only adult aquatic insects without open spiracles are the minute *Idiocoris* and *Paskia*, which live in one of the two lakes that are least likely to have dried out completely for many millions of years.

Throughout the Mesozoic, the rise of the angiosperms must have permitted the development of a modern marginal flora, which provides protection against excessive predation by fish and a place where insect predators may lurk unseen while waiting for the appearance of their own prey. The early immature aquatic insects seem to have had gill-plates, producing a simple current used in dermal respiration. Kukalová-Peck (1978), reviewing the many theories put forward as to the origin of the insect wing, makes a clear case for regarding wings and the gill-plates of Ephemeroptera as serially homologous, e.g., in an organism such as the Permian mayfly nymph, *Kukalova americana* (Kukalová 1968). She is, however, wary about attributing an aquatic habitat to the ancestor of all the

Pterygota. The earliest such ancestor presumably continued to moult throughout life without any sharp break in form at a particular metamorphic moult. There are several hypotheses as to the value of a series of lobes arising from the first thoracic segment nearly to the end of the abdomen, some not involving an aquatic stage. However, the development of a clear-cut metamorphic moult at which the lobes on the second and third thoracic segments become functional wings is consistent with a change of environment from water to air, as in the penultimate moult of a mayfly. So there may be an evolutionary connection here.

From the serial homology so obvious in the *Kukalova* nymph, we may reasonably expect at least the first aquatic insects to have had gill-plates, if not tracheal gills. As the phanerogamic littoral vegetation developed, underwater bugs or Nepomorpha (Popov 1971)—and doubtless some of the families of water-beetles—evolved. A second kind of aquatic respiration with an airstore permitted adults as well as nymphs or larvae to live underwater, and such insects were clearly prone to occupy some of the new niches offered by a rich marginal zone of angiosperms. The extensive haptobenthos associated with these plants would be a convenient source of food, perhaps better than the plants themselves. The late appearance of the diatoms suggests that the haptobenthos, which must have existed as a layer of colorless and blue-green bacteria far into the Precambrian, underwent considerable further evolution throughout the Palaeozoic. The development of a community capable of supporting a fairly rich microfauna would have added to the nutrient value of the so-called universal freshwater pabulum.

THE DINGINESS OF FRESHWATER INVERTEBRATES

One further aspect of this story seems ripe for investigation. Freshwater animals are notoriously dingy in color, as E. M. da Costa (1776), noticed more than 200 years ago. One of the brightest colors found in limnetic animals is the brilliant red of some planktonic copepods, which Hairston (1976) has shown has a purely physiological function, providing protection against excessive short-wave solar radiation. Among larger invertebrates, a crimson polyclad in Borneo and a green opisthobranch on

some islands in the western Pacific are the most brilliant, but they are of relatively recent marine origin. Some leeches and some mayfly nymphs have charming color patterns, but they are relatively subdued. Among mollusks the most decorative are certain Neritidae, notably in the genus *Theodoxus*, which, like their marine allies, have porphyrin pigments in the shells (Comfort 1950).

The only reasonably clear cases of aposematic coloring are provided by the scarlet water mites, which can be unpalatable (Elton 1922, Popham 1948).³ Ellis and Borden (1970) found that blood worms were the least preferred kind of food in a considerable selection offered to *Notonecta undulata*, suggesting that chironomid larvae, having acquired hemoglobin for respiration, have evolved some impalatability as an appropriate counterpoise to their increased conspicuousness when discovered by a predator nosing about on a shallow bottom.

The very striking series of poisonous secondary compounds in the Dytiscidae and Gyrinidae go unadvertised, doubtless because the advantages of warning coloration are more than offset by the disadvantage a predator has in being conspicuous. However, at the surface a scintillating school of whirlgig beetles may be conspicuous enough to discourage experienced predators such as birds.

On land a large number of distasteful species owe their unpalatability to secondary compounds derived from their food plants. Such herbivorous species can safely develop warning coloration. In freshwater the apparent rarity of plants containing such compounds would probably rule out this particular strategy. It would be interesting to know whether the species of *Donacia* feeding on Nymphaeaceae sequester alkaloids from their food plants, as the beaver feeding on the same plants appears to do.

There may be further reasons for the drabness of most freshwater animals. In quiet water, eddy diffusivity is likely to be lower than in air, so that a repulsive odor may be as effective a localized and permanent warning as a bright color, except perhaps for very small mobile animals, such as watermites. The work of Popham (1948) suggests that poor color vision and poor learning capacity may also play a part. Most aposematic coloration on land is directed against birds with superior color vision and adequate learning capacity.

³C. Kerfoot, personal communication.

Except among fishes, there is no certain development of epigamic coloration in freshwater animals. The backswimmers of the western American subgenus *Erythronecta* show some sexual dimorphism in the color of their hemelytra, the black and red females being the most brilliant of all aquatic insects. Though there is evidence that in *Notonecta undulata* males find their mates by sight (Clark 1928) and that part of the compound eye of *N. glauca* Linnaeus is sensitive to differences in color (Rokohl 1942), it is by no means certain that red and black hemelytra, seen from below against the sky and obscured by a silvery air-store, would provide a very powerful sexual stimulus. Except in the largest and clearest lakes, in which most of the more spectacular freshwater fishes having epigamic colors are found, the water may have always had just sufficient brown organic stain to dull the kind of brilliance associated with mating behavior on land.

None of these explanations is probably adequate by itself to account for the chromatic characteristics of the freshwater fauna. Taken together, they doubtless provide, in some cases, a partial explanation. Certainly, our knowledge of aquatic insects is still not great enough to enable us to think about them satisfactorily.

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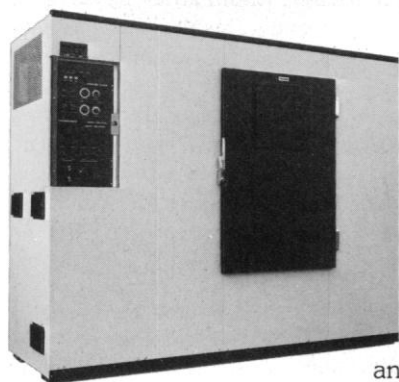
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