

Did the first insects live in water or in air?

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We evaluate the arguments and evidence for a terrestrial vs an aquatic origin for the Insecta. The evidence falls into three categories: (1) evidence that does not support one view more than the other; (2) speculative evidence, which should carry little weight; and (3) evidence that does support one view more than the other. Category 1 includes evidence from locomotory and osmoregulatory systems; plausible functions have been proposed for 'protowings' in both aquatic and terrestrial environments, while locomotory and osmoregulatory mechanisms of insects shed little light on their origins. Fossils, phylogenetic speculation, gill structure and life histories fall into category 2, in which, although speculative, the evidence favours a terrestrial origin. The earliest fossil hexapods were apparently terrestrial and unequivocally aquatic hexapods do not appear until 60–70 million years later, while sister-group relationships point to a terrestrial life style from at least the Hexapoda–Myriapoda stem group. The great variation in gill structure, even within orders, suggests convergence, and the more or less completely aquatic life histories are better interpreted as steps towards independence from land, rather than signs of an aquatic origin. Category 3 includes evidence from the tracheal system. In order to have evolved in water, a tracheal system must have first invaginated, then connected with the body wall for gas exchange with the water, and thirdly connected with the internal organs. It is difficult to envisage functions for the first two stages; on the other hand, the system could have readily evolved on land by invagination of respiratory surfaces, and then have been modified to effect gas exchange in water via gills.

ADDITIONAL KEY WORDS:—Insect evolution – aquatic/terrestrial habitats – fossils – phylogeny – tracheal system

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INTRODUCTION

One of the fundamental questions in the study of the evolution of life has been how the transition from aquatic to terrestrial life styles occurred (Panchen, 1980; Little, 1983, 1990; Chaloner & Lawson, 1985). Considerable debate has been devoted to the group of vertebrate animals (lung fishes or lobe-finned fishes) that made the transition, and whether it was made from marine or freshwaters (Chaloner & Lawson, 1985), and a similar debate is in progress on the other major group terrestrial organisms, the hexapods. Recent advocates of a terrestrial origin for hexapods include Wootton (1972), Hinton (1977), Manton (1977), Little (1983, 1990), Eriksen *et al.* (1984), Hynes (1984), Resh & Solem (1984) and Messner (1988). This view implies that there was a period of terrestrial evolution between the last marine ancestors and the first hexapods and that the adoption of a freshwater life style by insects was developed secondarily, after the hexapod form was complete. This contention is supported by the form of a number of systems, but the tracheal system provides the basic and strongest evidence.

An alternative view, that the first hexapods were aquatic, at least as juveniles, has had a long history, but has more recently been advocated by Riek (1971), Kukalova-Peck (1978, 1983 and, less emphatically, 1987), Stys & Soldan (1980) and Toms (1984). The evidence used in support of this model includes: the allegedly primitive nature of those orders of insects in which all species have an aquatic larva (Ephemeroptera, Odonata, Plecoptera, Megaloptera and Trichoptera), orders that we hereafter refer to as the BASIC-5*; large numbers of fossil Monura in aquatic deposits; the presence of a caudal style in only the most primitive of the Recent insects; and lack of spiracles on abdominal segments 9–11. However, the driving forces behind this view are acceptance of a sister-group relationship between Crustacea and Tracheata (Myriapoda + Hexapoda), and a hypothesis of wing origin from leg exites, structures seen to be homologous with mayfly gill plates. Thus, Kukalova-Peck (1987: 2342) argues that 'protowings evolved from appendages *as old as the leg* . . . and must have been engaged in some energetic function . . . long before the Devonian . . . when only water was inhabitable'. This function is therefore seen to be aquatic respiration, which is 'a common function of the upper leg exites of living Crustacea' (Kukalova-Peck, 1983: 1634). Thus, protohexapods are seen as necessarily being aquatic from the Crustacea–Tracheata stem-group through to the Pterygota. What this aquatic environment was is never clearly defined, but the C-T stem-group must have been marine. However, given the fact that larvae of the BASIC-5 now inhabit freshwater, the aquatic model implies that propterygotes, at least, lived in freshwater.

In this paper we evaluate the arguments on both sides of the debate, focusing attention on what is known, as opposed to what is conjecture. While it is important to have scenarios of evolutionary change, it is our opinion that these must be firmly based on what we know of how systems currently work. Thus we have grouped the evidence into three categories: (1) evidence that does not support one view more than the other; (2) speculative evidence, which should carry little weight; and (3) evidence that does support one view more than the other.

*Kukalova-Peck (1983: 1633) considers that the sysyrid Neuroptera and the gyrinid Coleoptera also probably have primitively aquatic larvae.

INCONCLUSIVE EVIDENCE

Locomotory systems

Although some authors (e.g. Matsuda, 1981) contend that flight in insects evolved more than once, the weight of evidence supports a single origin (Kukalova-Peck, 1983, 1985). The traditional view of wing origin in a terrestrial environment is embodied in the paranotal lobe theory. According to this theory, wings began as fixed lateral tergal outgrowths, the paranotal lobes, which were initially present on all post-cephalic segments, but were later lost from the abdomen and prothorax (Wootton, 1986). These outgrowths could have functioned as glide planes, enabling insects to descend in a stable manner from elevated positions (Hinton, 1963; Flower, 1964). However, Wootton (1986) concludes that Kukalova-Peck's (1983) movable exite theory is more plausible than the paranotal lobe theory and, if this should be correct, then a terrestrial function for these exites, prior to their use in flight, is required if the terrestrial model is to hold up. Possible functions that have been proposed are: signalling devices, stabilizers in free fall, or protective covers for legs or spiracles (Wootton, 1986), thermoregulatory structures (Kingsolver & Koehl, 1985), or to improve locomotion during short leaps (Kukalova-Peck, 1987). These functions are unfortunately necessarily speculative, but they are plausible speculations, and no less so than the conjecture that protowings originally functioned as gills. Indeed, the gill theory has, in our opinion, a number of weaknesses. For example, it is deficient in providing an explanation of how insects survived the transition periods when the gills would have been subject to desiccation on land.

Riek (1971) argues that the presence of a 'caudal style' in only the 'most primitive Recent insects' indicates that the ancestral insect was an active swimmer, and 'would have had at least the abdominal appendages modified for swimming'. He then argues that these became gills when insects left water for part of their life and developed tracheae, which 'penetrated into the abdominal swimming paddles . . . of the immature aquatic stages', resulting in something like a mayfly larva.

Riek has mayflies developing from trilobitomorphs. However, if we accept the more widely accepted phylogeny of myriapods, entognaths, apterygotes and pterygotes (see later), terrestriality would have had to have developed no less than five separate times in order to accommodate this single morphological character. Flexion of the abdomen as an escape reaction could well have developed in water, but it works on land as well; for example, in the archaeognathan *Petrobius brevistylis* Carpenter (Manton, 1977: 337).

We believe that a more satisfactory approach is provided by Hughes & Mill (1974: 335-6): 'Insects evolved from a myriapodan stock, and from the locomotory point of view they represent the final stage in a process of limb reduction . . . movement is characterized not only by its rapidity of forward progression, but particularly by the rate at which direction can be changed . . . they are land creatures which have successfully invaded the aquatic environment . . .'. Larvae of the BASIC-5 are all hexapodous and use a conventional walking gait as their normal locomotion. Modification of these walking legs as swimming paddles in aquatic insects occurs only in insects that move between the substrate and the surface to replenish air supplies (Hemiptera, Coleoptera) or for adult emergence (Trichoptera). Swimming by larvae of the BASIC-5 involves undulations (lateral or vertical) of the abdomen (often

aided by hair-fringed or flattened caudal processes), or expulsion of water from the anus (a corollary of rectal breathing) in Anisoptera, mechanisms that are generally used in escape behaviour rather than normal locomotion. Thus, although larvae of the BASIC-5 have a terrestrial style of locomotion, they move in ways not dissimilar from those of benthic macruran Crustacea, and cannot be said to be maladapted for aquatic locomotion. We are left to conclude that locomotory mechanisms of aquatic insects shed little light on their origins.

Osmoregulation

In order to survive, freshwater insects must replace salts, but must eliminate water; saltwater insects face water loss, but must eliminate salts; terrestrial insects must replace water (like saltwater species) *and* salts (like freshwater species). Thus, the osmoregulatory mechanisms shown by terrestrial insects cannot be the same as freshwater species or saltwater species, and so cannot throw any light on the life style of their ancestors. No matter where insects evolved, in order to live on land now they have to use osmoregulatory mechanisms appropriate to the terrestrial environment. In fact, insects appear to be very adaptable in this regard, and so it is impossible to sort out the ancestral character state of the osmoregulatory mechanism.

However, Little (1983, 1990) has considered the physiological implications of the colonization of land by various routes, and argues conclusively that the myriapod-insect line became terrestrial directly from the sea: 'most insects and myriapods are small, and if such forms had evolved in fresh water it seems likely that their osmotic pressure would have dropped radically, as in the smaller crustaceans. The fact that it has, on the contrary, remained high strongly suggests a marine origin' (1990: 78). The chelicerates, for which there is no disagreement on a direct marine origin, have similar compositions of body fluids. Furthermore, tolerance mechanisms are extremely well developed, and it is more likely that these would have evolved in the variable conditions of the marine littoral zone than in a freshwater one. Undisputed freshwater origins are associated with regulatory rather than tolerance mechanisms.

SPECULATIVE EVIDENCE

Fossils

Shear (1991) provides a review of the Palaeozoic fossil record of terrestrial (i.e. non-marine) ecosystems and the earliest occurrences of recognizable, relevant and apparently terrestrial arthropod taxa are summarized, along with ages and depositional environments, in Table 1. Unfortunately, this record is 'clearly grossly incomplete and yields only a distorted picture of the situation that must have existed' (Rolfe, 1980: 151). In addition, fossil evidence is open to various interpretations based on the identity of fossils and their age, theoretical inferences from the fossils and the nature of depositional environments inferred from sediments and associated fauna and flora.

Owing to the nature of preservation and preparation techniques, quality of fossils is highly variable, and often poor. It is essential when basing hypotheses on these specimens, that we acknowledge the strength of the identification upon

TABLE 1. Earliest occurrences of probable terrestrial arthropod fossils

Site	Date (Myr)	Habitat	Organisms	Reference*
Gilboa (U.S.A.)	Givetian, Devonian (about 376–379)	Delta, with fluvial transport, but no evidence of tidal influence	Pseudoscorpion, <i>Gilboarachne</i> , <i>Gelasinotarbus</i> , <i>Acutatarbus</i> (Trigonotarbid), <i>Devonobius</i> (Chilopoda), <i>Proctothonus</i> , <i>Devonacarus</i> (Acarina), <i>Aranea</i> (?), <i>Archaeognatha</i>	9, 11, 12, 13, 14, 15, 16
Alken-an- der-Mosel (Germany)	Emsian, Devonian (about 390)	Shallow brackish lagoon, emergent and marginal vegetation, flooded at high tide	<i>Eoarthropleura</i> (Arthropleurid), <i>Alkenia</i> , <i>Archeomartus</i> (Trigonotarbid)	17, 18, 10
Gaspé (Canada)	Emsian, Devonian (about 390–392)	Swamp-like environment with fluvial transport	<i>Archaeognathan</i> †	8
Rhynie (Scotland)	U. Emsian (?) Devonian (about 400)	Bog or lake shore	<i>Rhyniella</i> (Collembola), <i>Palaeocharinus</i> , <i>Palaeocharinoides</i> (Trigonotarbid), <i>Protacaris</i> (Acarina), <i>Palaeoeceniza</i> (Arachnida)	2, 3, 4, 5, 7, 10, 19
Old Red Sandstone (Britain)	Gedinnian (?) (about 405)		Abundant Myriapods, <i>Archidesmus</i> , <i>Kampecaris</i> , <i>Necrogammarus</i>	10
Shropshire (England)	Lludlowverian U. Silurian (about 414)	Beach or mud flat with fluvial influence	Trigonotarbid arachnid and Chilopoda	1, 6

*1, Bowler (1990); 2, Crowson (1970); 3, Greenslade (1988); 4, Hirst (1923); 5, Hirst & Maulik (1926); 6, Jeram, Selden & Edwards (1990); 7, Kühne & Schlüter (1985); 8, Labandeira *et al.* (1988); 9, Norton *et al.* (1988); 10, Rolfe (1980); 11, Shear (1991); 12, Shear & Bonamo (1988); 13, Shear, Schwaller & Bonamo (1989); 14, Shear *et al.* (1989); 15, Shear *et al.* (1984); 16, Shear *et al.* (1987); 17, Störmer (1970); 18, Störmer (1976); 19, Whalley & Jarzembowski (1981).

†The authenticity of this fossil has been questioned by Jeram *et al.* (1990).

which we depend. The identification is in turn dependent on condition of the fossil. Questionable identifications, then, should be handled with caution or ignored.

Theoretical inferences, such as those based on cladistics, are inherently subject to change as the acceptance or form of theory changes. It is essential to be aware of the basis of such inferences. As an example we can take the claim that Insecta originated in Ordovician or early Silurian times (Kukalova-Peck, 1987). It is based on the existence of *Archidesmus* and *Necrogammarus* in Upper Silurian rocks and Lower Silurian 'myriapod-like tracheates' from Wisconsin. If we accept the identifications of these questionable fossils, cladistic theory requires the co-existence of hexapod ancestors (which need not have been hexapods). Hence the Ordovician or early Silurian origin of hexapods. Should systematic theory change in the future, so would this inference.

Care must be exercised in identifying the nature of the depositional environments and in assessing the taphonomic changes that might have occurred in the fossils. The vast majority of fossils are preserved in aquatic situations, usually fresh or brackish water, but this cannot be taken to indicate an aquatic origin of hexapods (*Australopithecus* fossils in lacustrine sediments along Lake Turkana have never been interpreted as implying that early hominids were aquatic!). Nor can taphonomic pronouncements be speculative; they must be based on firm evidence (Wootton, 1988).

Wootton (1988) discussed the difficulty of identifying aquatic features in fossil hexapods, and it is almost as difficult to identify terrestrial characteristics with certainty. The terrestrial nature of the taxa in Table 1 is usually established on the basis of a relationship with more recent wholly terrestrial taxa. However, there are several weaknesses with this approach. Most of the material is fragmentary (*Rhyniella*, and all Gilboa, Shropshire and Gaspé specimens), and while fragments are usually recognizable at the level of class and sometimes order, generic epithets often merely reflect the need to assign a binomial to the specimen for purpose of discussion, and familial placement is rarely possible. Furthermore, even if taxonomic placement is correct, more recent forms need not live in the same habitat as older forms, viz. the revelation that the earliest scorpions were apparently aquatic (Kjellesvig-Waering, 1986), and yet need not show obvious change in structural features related to the transition from aquatic to terrestrial habitats. Thus, the terrestriality of the Rhynie, Gilboa and Shropshire trigonotarbid arachnids is inferred primarily from the knowledge that Carboniferous trigonotarbids were terrestrial. This is based on the presence in the later specimens of book lungs, which are restricted to terrestrial taxa and apparently cannot function in aquatic situations. Identifiable book lungs are not shown by the Silurian/Devonian specimens, perhaps because they were not preserved or perhaps because they simply did not possess them. However, equally, there is no evidence that these forms were definitely aquatic; recognizably freshwater taxa do not appear until the Upper Carboniferous with the advent of Odonata and Ephemeroptera (Wootton, 1988).

All known Lower Devonian locations are within 10 degrees of the equator and contain similar sized plant and animal taxa. We suggest that these observations imply that neither dispersal nor niche specialization has progressed very far, and therefore that we are examining sediments of an age close to the origin of hexapody. Defining a window of likely origin may be helpful as a guide to future research into early terrestriality, both in plants and animals. The youngest age is

defined by first occurrences in the fossil record, and theoretical inferences based on those occurrences. The oldest date for the origin of hexapody is more problematical. But if the first hexapods were terrestrial (although it is not impossible that the first hexapods were marine, none are yet known to have been) then the oldest date would be suggested by the earliest development of terrestrial environments. Chapman (1988) discusses this in terms of plants and the dependence on oxygen of biochemical pathways for synthesis of lignin (for support), cutin (for waterproofing) and phenylpropanoids (for screening ultraviolet radiation). Estimated development of oxygen partial pressures supporting these biochemical pathways was between 700 and 570 Myr ago. Earliest fossil indication of terrestrial life is taken from soil development and the appearance of thick-walled trilete spores and tracheids in palaeo-palynological preparations. The earliest palaeosols are apparently of Precambrian age (Retallack, 1992, in Gray and Shear, 1992), while thick-walled trilete spores first appear by late Silurian (Llandoveryian) and the first uncontested tracheids are of the same age. Thus, our current best estimate for a window for the development of early hexapods and their immediate ancestors is late Precambrian to late Silurian. Efforts should be concentrated on locating terrestrial and freshwater deposits within this window, and sampling for arthropod fragments.

In summary, the earliest (Lower Devonian, 400 Myr ago) fossil hexapods are all very small (< 5 mm). They are also wingless, subtropical-tropical, in terrestrial, but wet, marginal marine habitats, and associated with terrestrial plants (Labandeira, Beall & Hueber, 1988). Terrestrial arachnids and myriapods also occur in these assemblages and the implication is that terrestrial arthropods must have been established much earlier. This does not conflict with the evidence for the availability of suitable habitats because, contrary to Kukalova-Peck's (1987) statement, biogenic soils (palaeosols) *were* present in the Cambrian at least, possibly the Pre-Cambrian. The first clear fossil evidence for aquatic insects is the Lower Permian, when they seem to have filled the small predator role (Wootton, 1972). There is no good evidence that fossil Palaeoptera had aquatic juveniles (Wootton, 1972), and the observation of *Monura* in aquatic deposits (Kukalova-Peck, 1983) tells us nothing of their life style. In fact Shear & Kukalova-Peck (1990: 1817) now say that these specimens may have lived on vegetation above water, 'climbing up and down emergent stems'.

Phylogeny

Phylogeny is necessarily conjectural, but various pieces of evidence, including the fossils from the Burgess Shale, have been used to suggest that arthropods arose repeatedly from non-arthropod ancestors (Willmer, 1990). However, recent studies in limb morphology (Emerson & Schram, 1990) and molecular systematics (Patel *et al.*, 1989) argue convincingly for the traditional monophyletic model. Thus, although we believe that the logic of Willmer's argument is suspect and Shear (1992) has conclusively summarized the recent evidence in favour of the monophyletic view, the debate over the relationships between the major arthropod groups, started by Tiegs and Manton (1958), continues.

Boudreaux (1979), Kristensen (1981), Hennig (1981) and Kukalova-Peck (1987) all agree on monophyly of the hexapods; all except Kukalova-Peck agree

on monophyly of entognaths; all agree on monophyly of ectognaths; all agree on a sister-group relationship between Archaeognatha and Dicondylia; and all agree on a sister-group relationship between Thysanura and Pterygota. Boudreaux and Kristensen do not acknowledge Palaeoptera, while Kukalova-Peck and Hennig do. Kukalova-Peck (1987) stops at this point, but the others do not see any close relationship among the BASIC-5. Thus, on the basis of the sister-group relationships that are agreed upon, the most parsimonious hypothesis would be for a terrestrial life style from at least the Hexapoda-Myriapoda stem group, because all of the branches of this lineage are terrestrial today, all except the Pterygota exclusively so. Kukalova-Peck's (1983) alternative scenario is unfortunately brief. She argues that 'ancestral tracheates possibly had aquatic juveniles and amphibiotic adults already when the split occurred into myriapods and insects... Myriapods and insect-endognaths independently and gradually became terrestrial in adults and juveniles. Thysanuroids maintained aquatic juveniles in the Paleozoic [but see the comments on Monurans above], but changed to a fully terrestrial life in the Mesozoic. Most generalized pterygote orders retained aquatic juveniles with a "closed" tracheal system... until present times'. We disagree that 'most generalized pterygote orders' have aquatic juveniles (the BASIC-5 do not form a majority among generalized orders, no matter how the latter are defined), but this is a minor point. Our main concern with this scenario is the very large number of independent, fully terrestrial offshoots from the ontogenetically amphibious hexapod stem that would be necessary. If we restrict the analysis to extant hexapod orders and follow Kristensen's (1981) phylogeny, we count 11–16 such offshoots (Fig. 1). If certain families within Coleoptera and Neuroptera (see footnote, p. 32) have maintained the primitive amphibious life style and the analysis has to be extended to the family level, the number increases further. Also, there are many pterygote taxa that are widely acknowledged as having invaded freshwater from dry land—Hydrocorisae, Hydradephaga and Nematocera, plus several families of Polyphaga, Brachycera and Lepidoptera; if the propterygotes had aquatic larvae, these secondarily

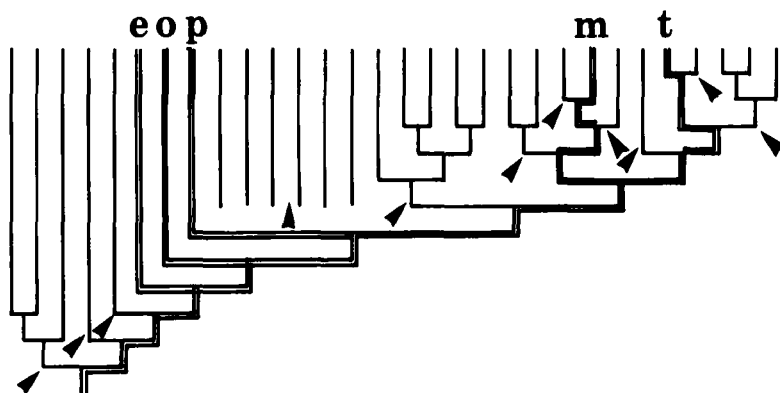


Figure 1. Kristensen's (1981) phylogeny of the hexapod orders, modified to show the minimum number of fully terrestrial offshoots (arrows) from the ontogenetically amphibious stem required by the aquatic model. The possibly polyphyletic terrestrial Polyneoptera are treated as though they are monophyletic. The stem is shown as a double line, running directly to the BASIC-5—Ephemeroptera (e), Odonata (o), Plecoptera (p), Megaloptera (m) and Trichoptera (t). See text for further information.

aquatic taxa, having perfected their terrestrial preadaptations in water and colonized land, must have then returned to the habitat which their ancestors vacated.

Adding the BASIC-5 to these secondarily aquatic taxa is not only phylogenetically parsimonious, but also preserves the predominant pattern of invasion of freshwater habitats from dry land. In fact, physiological, morphological and phylogenetic evidence suggests that arthropods have been able to colonize freshwater more easily from the terrestrial environment than from the marine, and this raises a further point. If the Crustacea and Tracheata are sister-groups (Kukalova-Peck, 1983), as the majority opinion seems to hold, then the tracheate line must originally have been marine. Given that the BASIC-5, considered in the aquatic model to represent the primitive hexapod mode of life, live only in freshwater, proponents of an aquatic origin must provide an explanation for how this marine to freshwater transition occurred. We are concerned by the lack of any reference to this transition in the scenarios advocating an aquatic origin.

Gills

Eriksen *et al.* (1984) list eight (non-exclusive) respiratory options for aquatic insects. At first glance it may appear significant that the orders that constitute the BASIC-5 have developed only one option. However, the significance is unlikely to be phylogenetic for, while they all possess tracheal gills, they display great variation in form and placement on the body, even within a single order. For example, in the Odonata there are four fundamentally different types of gills (Norling, 1982). Furthermore, tracheal gills are also widespread in the aquatic Hemiptera, Coleoptera and Diptera, and are found in the aquatic Lepidoptera, the latter demonstrating that tracheal gills need not indicate a very old commitment to the aquatic habitat (Hynes, 1984). Shepard & Stewart (1983), in a study of the so-called gills of Plecoptera larvae, even argue that gas exchange was not the original function of these structures, as it may well not have been in Odonata (Pritchard, unpublished observations). And finally, larvae of at least some Odonata and Megaloptera have functional spiracles (Hamilton, 1940; Hinton, 1947; Cuyler, 1958). All of these points suggest that the evolution of gills has been convergent, merely reflecting a common solution to the problem of aquatic respiration (Hynes, 1984).

Life histories

The life histories of 'aquatic insects' are very varied, but it is striking that there are no confirmed examples of completely aquatic life cycles (in which no stage has a terrestrial existence) among the BASIC-5. A wingless adult stonefly was reported to occur in the depths of Lake Tahoe by Jewett (1963), and larval mayflies, stoneflies and caddisflies have been taken from very deep water (32–100 m) in Lake Superior (Selgeby, 1974). Flightless caddisfly adults are recorded from Lakes Baikal (Kozhov, 1963), Tanganyika and Titicaca (Marlier, 1962; Beadle, 1981), but adults of *Baicalina bellicosa* in Lake Baikal do attempt to fly, fail, and then swim to shore and oviposit on exposed rocks. Barton & Smith (1984) consider these examples to be steps towards independence from *land*,

rather than signs of an aquatic origin, as is the shortening of the adult stage in all mayflies. Pharate adult Chironomidae that reproduce parthenogenetically (Hinton, 1946) demonstrate a way in which terrestrial reproduction can be circumvented and a completely aquatic life cycle can be achieved.

STRONG EVIDENCE

The tracheal system

The aquatic model requires that tracheae developed in water. Although Beament (1961) pointed out the advantages of the oxygen distribution capacity of a tracheal system to aquatic insects and proposed that aquatic air-breathing could have preceded terrestrial water-proofing, he did not propose how a tracheal system might have evolved in water. To explain this, Kukalova-Peck (1983) refers to the hypothetical evolutionary mechanisms footnoted by Stys & Soldan (1980: 432), which bears repeating in full: 'The tracheal system of proterygotes need not have evolved in [a] terrestrial environment. The course of events might have been as follows: (a) diminution in the size of the aquatic pre-insect resulting in reduction of its circulatory system (and eventually also of previously present gills); (b) increase in its size accompanied by a necessary strengthening of the cuticle for attachment of stronger muscles resulting in insufficiency of the cutaneous respiration and development (or increase in size) of gills . . .; (c) further increase in size necessitating the evolution of tracheae forming an efficient system for oxygen transportation from gills to body tissues and for fastening of inner organs (in this stage permanently apneustic spiracles would function only as sites of embryonic or early postembryonic invagination of tracheal tissues and of pulling out the tracheal intima after each moult). Both prespiracles and the tracheal system would then be important and immediately ready preadaptations for a shift of proterygotes to at least partially terrestrial life. Most of the modern larvae of the ontogenetically amphibious orders are provided with tracheal gills, a well developed tracheal system and rudimental spiracles, and thus correspond to the suggested anagenetic stage (c)'. We find this proposed sequence illogical and teleological, and, in fact, lacking a scenario for the very phenomenon that it is purporting to describe—the development of a tracheal system (other than that such a development was necessary).

On the other hand, the tracheal system can easily be envisaged to have evolved on land by invagination of respiratory surfaces. Tracheal systems have evolved at least four times (Onychophora, Chelicerata, Isopoda and Tracheata—Boudreaux, 1979) or as many as ten times if accessory tracheal organs are taken into account (Ripper, 1931), and always in association with a terrestrial mode of life; no fully aquatic arthropods (i.e. Trilobita, Merostomata and most Crustacea) have or had tracheae. In desiccating environments, increased surface area of respiratory surfaces can only be accomplished internally, but even small invaginations (which is how an arthropod tracheal system has to start) would have adaptive value in facilitating gas exchange while reducing water loss. Further invagination and branching would allow more rapid transport of gases to and from the tissues and an increase in body size. By contrast, any explanation for the origin of tracheae in water that we can think of has to be teleological.

On land, a single point of invagination will allow the system to work (Fig. 2A). But in water the tracheal system does not work at its points of

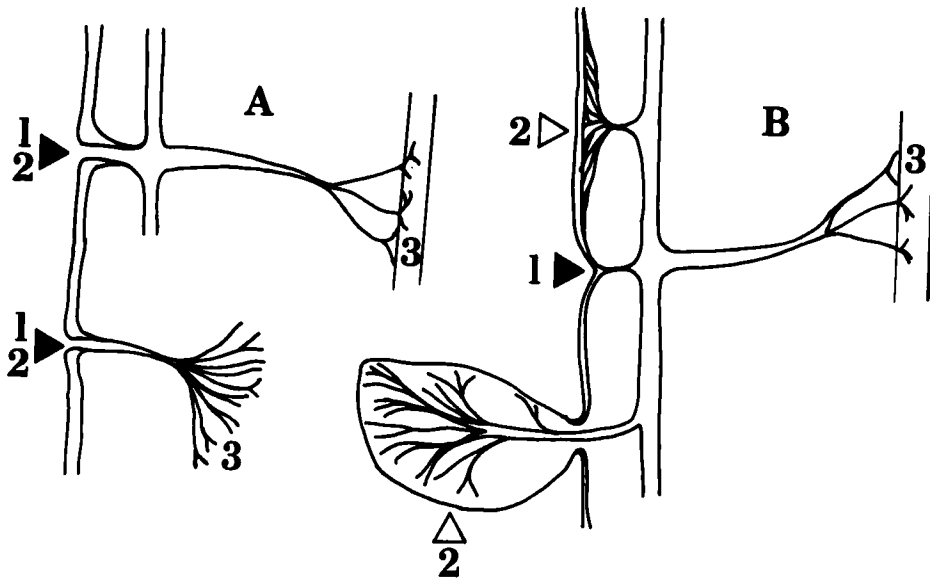


Figure 2. A. Upper portion shows the basic detail of the tracheal system of a terrestrial insect; lower portion shows that of an onychophoran, a terrestrial isopod, or an arachnid. B. The tracheal system of an aquatic insect; upper portion with simple cutaneous respiration, lower with evaginated gills. In order to develop and function, an arthropod tracheal system requires (1) a point of invagination, (2) a point for oxygen uptake, and (3) a point for oxygen delivery. A simple invagination provides all three in a terrestrial arthropod, but three separate and sequential events must occur in an aquatic arthropod.

invagination; it must first invaginate, then make connection with the body wall for gas exchange with the water, and thirdly make connection with the internal organs (Fig. 2B). Like Paley's (1828) eye, only when fully formed is the system functional; there is no advantage to be gained from mere invagination, nor from invagination plus connection with the body wall. However, a complete tracheal system, developed on land, would be a preadaptation for efficient delivery of oxygen from the body wall (with or without gills) to the active tissues in an aquatic insect. This is clearly shown in insect groups that are universally acknowledged to have secondarily developed an aquatic life style, such as aquatic *Pyrilidae* (Lepidoptera) or aquatic *Tipulidae* (Diptera). The latter show, even with the single genus *Tipula*, a range of respiratory mechanisms from terrestrial species breathing air through open spiracles, to aquatic species breathing air at the water-air interface, to terrestrial species with open spiracles *and* tracheal plexi under the body wall that perhaps function during times when the soil is flooded, to aquatic insects with sealed-off spiracles and tracheal plexi under the body wall (Pritchard & Stewart, 1982). And, on a shorter time scale, Harnisch (1958) records the development of tracheal plexi under the abdominal body wall in larval *Zygoptera* that have lost their caudal gills. Clearly, it is a simple matter to make this connection if the tracheal system already exists.

CONCLUSIONS

(1) The functions envisaged for 'protowings' are unfortunately necessarily speculative, but plausible functions have been proposed for both aquatic and terrestrial environments.

(2) Osmoregulatory and non-flying locomotory mechanisms of terrestrial insects shed little light on their origins, but the former support a route from salt water rather than from fresh water.

(3) Fossil evidence suggests that terrestrial environments were present well before the time of hexapod origin. The earliest fossil hexapods were apparently terrestrial and unequivocally aquatic hexapods do not appear until 60–70 million years later.

(4) Adding the BASIC-5 to those taxa of insects that have *secondarily* invaded freshwater from dry land is phylogenetically parsimonious and leads to fewer physiological difficulties.

(5) While all of the BASIC-5 possess gills, they display great variation, even within orders. This suggests that the development of gills was convergent, merely reflecting a common solution to the problem of aquatic respiration.

(6) More or less completely aquatic insect life histories are better interpreted as steps towards independence from *land*, rather than signs of an aquatic origin.

(7) In water the tracheal system does not work at its points of invagination; it must first invaginate, then make connection with the body wall for gas exchange with the water, and thirdly make connection with the internal organs. On the other hand, a simple invagination of respiratory surfaces would be immediately functional on land.

(8) An aquatic origin for hexapods seems extremely unlikely. In contrast, a terrestrial origin is not disputed by any of the facts nor by any of the more firmly based speculations.

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