

On the skimming hypothesis of the origin of insect flight

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Abstract. The skimming hypothesis of the the origin of insect flight is considered in several possible scenarios. No scenario is found to be in agreement with available information about the insect fossil record and the environments of early insect evolution.

Key words: skimming hypothesis, insect flight, early evolution of insects.

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The skimming hypothesis of the origin of insect flight (MARDEN & KRAMER 1994; MARDEN 1995, 2001) gains growing popularity (RUFFIEUX et al. 1998, SHCHERBAKOV 1999; WOOTTON; KUKALOVÁ-PECK 2000). At the same time, its premises and consequences do not appear fully clear. The objective of this note is to help fill this lacuna.

Although not identical in details, the views of the creators and proponents of the hypothesis are consistent in that insect flight was preceded by, and developed directly from, the stage of skimming locomotion. The latter implies that (i) the immediate pterygote ancestor, like gerrid bugs, existed on the water surface relying on support received by their hydrophobic legs from the water surface film; (ii) unlike the water striders, its locomotion was air driven resulted from aerodynamically efficient movements of comparatively short airfoils (like in some short-winged stone- and mayflies), the wing precursors; and (iii) these precursors of the insect wings were limb appendages (usually homologized with the epipodite) inherited as such (i.e. free and movable) from an aquatic ancestor (though SHCHERBAKOV 1999 does not exclude possibility of epipodite to be incorporated temporarily into pterothoracic paranota and soon re-mobilized in accordance with the necessity of skimming locomotion).

The first problem with the hypothesis is that the water skimming and striding insects are by necessity comparatively small and light (like gerrid bugs; striding caddis flies can be heavier, but they use wings as additional support). In contrast, the earliest known (Namurian) pterygotes are large to very large (commonly one to several inches long), and even the smallest one, *Metropator pusillus* HANDLIRSCH, had its wing 8.5 mm long. Small fliers appeared only later in Carboniferous (the wing length of the smallest Carboniferous winged insect *Eodelopterum priscum* SCHMIDT is 4.6 mm, and of *Archaemioptera carbonaria* GUTHÖRL is 5 mm) and became gradually more and more common since Permian till now. This is in accord with the paranotal hypothesis of the insect wing origin (WOOTTON & ELLINGTON 1991), and not with the skimming hypothesis.

Insect flight origin under the skimming hypothesis can be envisaged in several scenarios. The first major dichotomy is if the ancestral wingless insect, or the insect ancestor, gained support from a solid substrate when breaking through the water surface film, or if it did so without such support. The latter alternative, that is an unsupported break through the surface film while passing from underwater to aerial epipleuston existence (Fig. 1), implies the evolutionary instant and complete ontogenetic shift from an aquatic stage with a hydrophilic integument to an aerial stage with hydrophobic integument, as it occurs in mayflies and mosquitoes. Development of anhydrophobic integument hidden under the hydrophilic one can be easily established in a gradual way using an intermittent epigeic stage where distinction between the hydrophobic and hydrophilic integument is not so crucial.

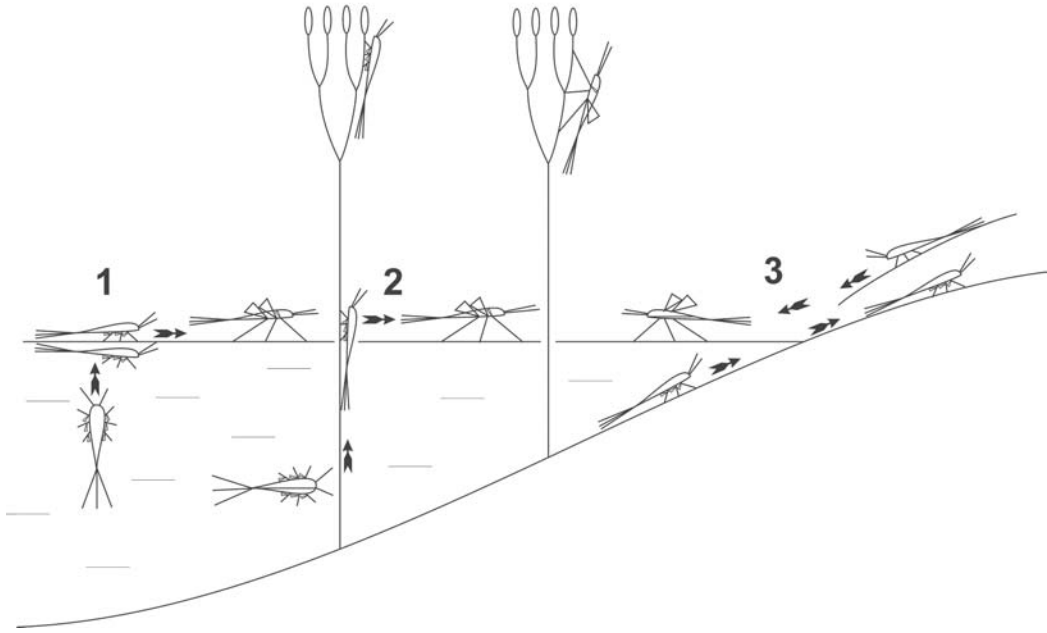
The case under discussion is different: it supposes a simultaneous transition, first, from an aquatic way of life to amphibiotic development, with an aerial epipleuston stage added to the end of ontogeny, and second, from a hydrophilic to a hydrophobic integument. This double transition is too complicated to evolve instantaneously, and yet it cannot evolve gradually, for the incompletely hydrophobic insect cannot break the surface film successfully and so is destined to die. So direct transition from an aquatic to an amphibiotic way of life with epipleuston aerial stage is unlikely for this reason also. However, there is another problem: such a transition would mean a case of metamorphosis, even if an incomplete one (as in mayflies, dragonflies and stoneflies). Incomplete metamorphosis is known in neither wingless insects, and reasons for its possible origin there are obscure at best.

The alternative scenario permits the ancestor to gain a support from solid substrate, either a bottom of water body or half-submersed plants, while moving from water into air (Figs 2, 3). It brings us nearer to the more customary hypothesis of transition from water into air via an epigeal stage, and enters another dichotomy: whether this stage was long or ephemeral. Of course, the matter is the extent of specific adaptation acquired at that stage rather than its absolute duration. Of primary importance here is that either the propulsory machinery used while in water was directly and immediately used to give the air thrust (Fig. 2), or there was a functional break, and in a sense the wing as a propulsory device appeared *de novo*, even if as a homologue of a propulsory organ of the aquatic ancestor (Fig. 3).

Enough evidence has accumulated that the insect wing is a homologue, even if partial, of a limb part of ancestor (e.g., RASNITSYN 1981). An epipodite is often named as the wing precursor, but it is a coxal appendage and so might correspond to the coxal stylus and not the wing. It is the pre-epipodite which is thinkable as possible wing homologue. Anyway, in all known examples the insect wings ontogenetically develop from pterothoracic paranota which are already present in apterygotes. This does not contradict the limb hypothesis of the insect wing origin, for a paranotum well may include ancestral limb tissue. It only implies that the hypothesis of the uninterrupted motility of the wing precursor (Fig. 2) infers at least a triple independent origin of pterothoracic paranota – in Archaeognatha, in Zygentoma and in stem group of all pterygotes with known immatures. Again this is not the last problem: although well motile, the pre-epipodite is a respiratory rather than a locomotory organ, and to become an airfoil generating enough thrust to move the insect over the water surface more efficiently than its legs, it needs deep transformation of not only, or rather not so much the appendage itself, as all the construction of the entire segment. It is not uncommon, and is therefore instructive that man-made air-driven boats, like the extant insect skimmers, have thrust machinery once designed for real flight and only secondarily adapted for gliding over water.

And this is still not enough. The most crucial question is, to my mind, what was the reason for ancestral winged insects (or for the Pterygote ancestor) to acquire the epipleuston habits. In other words, what they could find attractive there. I believe that not much: maybe the space for courtship and/or a possibility to find a way from one plant grown through water into air to another such plant or plant group. These plants might be attractive as a retreat or as a possible source of food, particularly the spores in sporangia. However, the energetically less wasteful water striding looks more appropriate and more easily available to satisfy both these attractions than water skimming. As to

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Figs 1-3. Three possible scenarios of the insect flight origin under the skimming hypothesis (see text for details).

hunting or scavenging, these attractions hardly existed before the winged insects appeared and became abundant: the pre-Namurian fossil record witnesses just absence of enough potential prey onto the water surface.

Also, the water surface was not really a safe place in that remote time: although the aerial predators were absent and water surface ones were restricted to chelicerates and possibly myriapods, underwater predators were plenty and dangerous for the epipleuston.

The last but not least evidence comes from taphonomy. The water skimming and water striding are most safe and efficient and so most probable to occur in the still water which is also taphonomically favorable (ZHERIKHIN 2002a). Absence of respective fossils through all the Paleozoic indicates very clearly that these ways of life are late in origin (ZHERIKHIN 2002b).

SHCHERBAKOV (1999) has modified the hypothesis and supposes that the skimming locomotion has appeared in running waters as an adaptation counterbalancing the downward drift of aquatic development stages by current. This scenario does not seem likely as well, because the downward drift is measured by kilometers, and to counterbalance it, the upward skimming locomotion must be unrealistically powerful and efficient in order to overcome the wind and current, as well as other dangers, for so long distance.

The last alternative, also proposed by SHCHERBAKOV, is a partial return to the hypothesis that the insect wing has originated due to re-mobilization of the ancestral limb part once incorporated into the paranotum (RASNITSYN 1981). This does remove some of the above problems but leaves intact the majority of them, and also it adds a new, purely hypothetical evolutionary step. Indeed,

paranota are a terrestrial adaptation, so SHCHERBAKOV's hypothesis implies that the wingless amphibiotic ancestor has left a terrestrial environment for an epipleuston is one. It might have started from still waters, but this is unlikely because of the absence of relevant fossils from the taphonomically favorable deposits of still waters. Otherwise the ancestor would need directly to have invaded the running waters which are adaptively unfavorable for the epipleustonic way of life and so leave little chance of success.

The above considerations imply that the surface film well could be regularly crossed by ancient wingless insects, particularly by the visitors of plants grown through water into air. Less likely is the existence of specialized film dwellers in those remote times, and still less that skimming locomotion might ever have originated starting from this way of life. Much more realistic seems the hypothesis that skimming locomotion descended from flight rather than preceded it.

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