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BOOK REVIEW

BRODSKY A.K.: THE EVOLUTION OF INSECT FLIGHT. Oxford University Press, Oxford, New York, Tokyo, 1994, XIV + 229 pp. ISBN 0-19-854681-5. Hardbound. Price GBP 55.00.

This book, translated from the author's Russian original, aims to be a comprehensive treatment of the structure, function and evolution of insect flight apparatus. The two main subdivisions are entitled "Basic principles of insect flight" (pterothoracic morphology and musculature, axillary apparatus, wing morphology, wing mechanics, flight aerodynamics, behavioural aspects), and "The evolution of insect flight" (origin of wings and flight, supposedly primitive flight types, origin of functionally two-winged flight, various types of flight improvements and adaptations, some general evolutionary considerations). Even from this short excerpt, you can see that the author's plan was very ambitious considering the difficult subject and current uncertainty and disagreement about many aspects of insect wings and flight, beginning with their evolutionary origin and the apparatus' component homologies.

"This book is not for easy reading at idle moments", says Brodsky in the Preface. Alas, he is correct. It was very difficult to get through, and few books have made me repeatedly read a paragraph so often. However, I am afraid that this was not solely due to the difficult subject, rather some of the ambiguity was undoubtedly caused by the author. If we consider two of this century's best known writers on general insect morphology, Snodgrass and Matsuda, Brodsky is certainly akin to the latter, lacking the clarity and didactic qualities of Snodgrass and overwhelming the reader with scattered bits of information. In the beginning of the book the reader may fear that the depths of the author's thinking are difficult to understand or that the previous pages were not read carefully enough, but towards the end the reader is inclined to think that the author simply wrote somewhat carelessly. While there is grammatic consistency, the logic is often difficult to follow. All too often the book reads like this: "Apples are round; on the other hand, however, strawberries are red, and potatoes grow underground". The author may explain why potatoes are important a few pages later, but may have first provided some incomprehensible messages about onions and plums. I found this to be most painful in the initial morphological chapters, but this may be explained by the fact that I am a morphologist.

The best parts of the book may be those on flight mechanics and aerodynamics, the author's main field of interest and, unfortunately, the part I am least competent to evaluate. The second part of the first subdivision deals specifically with these aspects, and they are also abundantly discussed in the second evolutionary part of the book. In places, discussion of other aspects appear to be merely subsequent additions to this core topic, and the short subject index, for example, is also largely restricted to the same field.

However, if there is a consistent philosophy behind the evolutionary considerations, I did not recognize it. Going back in time, Brodsky becomes a story-teller without defining sound rules for his speculations. Some of his "phylogenetic" statements are just lovely; for instance, on page 117 we learn that stoneflies "have retained a lot of primitive structural features, such as thysanuran-like nymphs...". And the evolutionary dialectics on p. 197 is simply irresistible: "The marked similarity in structure of the pterothorax between the Plecoptera and Megaloptera, on the one hand emphasizes the parallelism in their development and, on the other hand, allows us to regard both groups as a kind of 'starting point' in the evolution of the Polyneoptera and Oligoneoptera respectively." I really regret such rubbish thirty years after Hennig.

Let me exemplify some of my objections by using Brodsky's treatment of the fascinating evergreen issue of the origin and earliest evolution of wings and flight. In recent studies, the long-reigning paranotal theory suggesting that wings evolved from lateral notal outgrowths and that flapping flight was achieved via gliding appears to lose support in favour of theories postulating that some articulated appendages were employed as active protowings. Before I discuss this further, I ask the reader to distinguish strictly between two aspects: the morphological source of wings and the functional cascade through which flight was achieved. It

is not always acknowledged that these two aspects are largely independent and that the rejection of one aspect of paranotal theory does not necessarily involve rejection of the other aspect. If, for example, we conclude that protowings were primarily articulated, they could still be the paranota that acquired articulation earlier for some other purpose. If we are convinced that wings are of non-paranotal origin, they could still have been first used for gliding, whether or not they were primarily articulated. Please note that all articulated appendages must have once evolved from non-articulated appendages, and the dispute about wing articulation is limited to whether it originated after the origin of flight (in that case passive) for steering and/or wing folding, or whether it was acquired earlier for some other purpose and flight, either passive or active, followed. There is virtually nothing in the book on morphological wing sources, other than a mention of the epicoxal exite theory of Kukalová-Peck. Brodsky seems to support the widely upheld theory that wings are serially homologous with mayfly abdominal gill plates (but denies homology with the prothoracic outgrowths found in many Palaeozoic fossils); however, this tells nothing about the origin of either wings or gill plates. The following discussion will, therefore, concern only functional aspects.

In many places in the book, it is clear that Brodsky supports the direct origin of flapping flight using pre-articulated appendages; he considers all insect gliding secondary. I do not propose a different concept (after all, this is not the purpose of a book review), but I argue that he does not provide any strong arguments to support his view.

Brodsky (p. 2) argues that, while there have been several instances of transition from flapping to gliding flight, "a transition to flapping flight from gliding has never been documented". This is a logical flaw, equivalent to asking why life does not continue to originate from abiotic material today. It is indeed possible that all instances of gliding capabilities that we know or presume (in fossil Palaeodictyopteroidea, Odonata, Ephemeroptera, Neuroptera, or Lepidoptera) are secondary, but all of these insects are, or supposedly were, capable of *both* flight types. Thus, we do not know of any "exclusive glider" (and therefore cannot "document a transition to flapping flight from gliding"), but this is of no relevance because we obviously do not know the "initial flier". If it had been a glider, it would probably have disappeared quickly when more advanced flappers, or even combined flappers/secondary gliders, entered the scene, and the re-appearance of such a form would not be very likely with all those flying insects and later other creatures around. In any case, contrary to vertebrates, it seems that the event was never repeated in arthropods (let us disregard Matsuda's theory about independent origin of flight in dragonflies), and thus we have no parallels to judge from. In addition to being evolutionarily short-lived, it is likely that the transitional forms would be uncommon, since major evolutionary achievements probably did not occur in large populations. This may be the classical scenario of overcoming "difficult" evolutionary barriers, and flight certainly is one of these. We should finally accept the idea of "punctuated evolutionary equilibria" and stop wondering about missing links or, worse, claiming that we have found them when we obviously haven't. For this reason I do not understand why Brodsky first, correctly, warns that no fossil record is available to document the real beginnings of flight which may have occurred "somewhere between the Devonian and the Carboniferous" (p. 79, please note that we would be still deeper in the woods if we accepted the occurrence of thrips in lower Devonian which I find unbelievable, but see Kühne & Schlüter, 1985, *Entomol. Gen.* **11**: 91–96), and then (p. 82) concludes that gliding is secondary because "gliding and soaring are usual for large insects and require special adaptations, changes in the structure of the wings and axillary apparatus". Adaptations of what? Of a well-flying flapper's wing that is purportedly primitive although sufficient support for this premise is lacking. In regards to size, fossil records of the oldest known pterygotes from the upper Carboniferous are mostly at least moderately large insects; of course, this may not be important, but there is no support for the postulation that the first flying insects were small, which obviously would have been required for direct terrestrial origin of flapping flight without a gliding intermezzo (see also below). Brodsky repeatedly cites archedictyon (irregular meshwork between the main wing veins) as a primitive wing feature, but this feature is typical of large insects and is usually poorly developed or absent in small ones. Brodsky's treatment of the axillary apparatus is also mysterious: On p. 16 he describes and depicts a "generalized axillary apparatus". You may wonder what "generalized" means, but if you dreamed about having a groundplan, you are ruthlessly awoken on p. 117: "The articulation areas of stonefly wings are characterized by an extremely archaic structure. Their axillary apparatus

differs from the generalized one...". Consequently, the lack of a clear statement defining supposed groundplan characters (i.e., characters the wing should have possessed when it started serving flight function) gives rise to confusion and contradictions throughout the book. Claims like the one on p. 195 ("in the first winged insects, the tergum of the wing-bearing segment seems to have been equipped with all the structures necessary for flapping; that is, a complete set of sutures, sulci, and ridges") simply suggest that all structures needed for flapping flight evolved previously for an unknown purpose, about which we, in fact, do not care very much. I regard the latter as an unfair and unacceptable escape from the problem. Incidentally, there is a complete lack of comparison with apterygote insects. Neither I find a clear discussion of the *evolutionary* origin of wing folding; Brodsky considers the inability of folding in the recent Palaeoptera and some fossils secondary, and he possibly assumes that both articulation *and* folding originated for some other purpose before the origin of flight (this is not clear to me).

In several places Brodsky resorts to comparisons with flying vertebrates. I am not certain that this premise is entirely sound; however, if accepted, I suggest that just in Vertebrata we probably find examples of both types of flight origin. In my opinion there can be little doubt that flight originated via gliding in bats or pterosaurs (in birds this is uncertain) *even if the appendages used for gliding were primarily articulated*, while the possibility of a "non-gliding" flight origin may be evident in some fishes. Indeed, if we accept the "flapping first" theory then utilizing appendages primarily adapted for propelling the insect in or on the water is, perhaps together with ventilation in a broad sense, the only plausible explanation I have seen. This is because it is obvious that the system, in the moment when it was utilized for flapping flight, must have been sufficiently powerful and aerodynamically preadapted. The aquatic origin of flight would also help to explain the remarkable fact that so many supposedly basal pterygote groups (Ephemeroptera, Odonata, Plecoptera, Megaloptera s.l.) possess aquatic larvae, whereas known apterygote insects are terrestrial. Moreover, freshwater aquatic habitats are patchy and necessitate some effective means of passive or active dispersion. Brodsky suggests (p. 81) that the original functions of the wings might be "unexpected ones such as signalling or for holding eggs on the back". First, sexually specific structures and functions are disqualified as wing and flight predecessors since, obviously, both males and females fly. Second, while I have no problems with the competing gliding theory which seems to be evolutionarily "smooth", I do have problems with insects displaying so excitedly that they fly away (and with many other proposed models of terrestrial take-off via flapping). We should keep in mind that we are primarily interested in the function of *immediate* wing precursors.

To be fair, however, the discussion of the wing and flight origin is possibly the most problematical portion of the book because of the lack of factual support. I believe that many of the conclusions about evolutionary relations between various types of flight found in recent insects may be sound and these conclusions are largely based on Brodsky's original observations.

In summary, the main importance of this book is the cumulative data about flight of recent insects, and Oxford University Press should be acknowledged for publishing many of the author's original results, which were thus far available almost exclusively in Russian. The book should be read by specialists capable of sifting through the volume for useful information. Be prepared for difficult reading, and be suspicious when the author speculates about evolution. On no account can the book be recommended as a handbook (or even a textbook) on insect wings and flight.

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