NUMBER 628 JUNE 11, 1963

OCCASIONAL PAPERS OF THE MUSEUM OF ZOOLOGY
UNIVERSITY OF MICHIGAN
ANN ARBOR, MICHIGAN

MATING BEHAVIOR AND THE ORIGIN OF INSECT WINGS

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THE wings of insects, birds, and bats are each generally presumed to have arisen but one time. The wings of birds and bats are modifications of the forelimbs, and to understand their evolution one needs only to understand selective forces that could modify an appendage already provided with elaborate and complex musculature, probably transforming it through some sort of functional gliding stage. But the wings of insects are not homologous with any appendage in modern arthropods. They are outgrowths of the dorsal body wall, and they appear to derive at least some of their movements from muscles that formerly operated only the thoracic legs. It is difficult to reconstruct the conditions of their origin and the sequence of functional changes through which they had to pass before they became primarily organs of flight. Numerous hypotheses have been advanced, some of them in direct conflict with one another. Certain suggestions have seemed more reasonable than others, but none has been universally accepted or remained in favor for long. Recently, Wigglesworth (1963) has introduced a completely new hypothesis, the first new one in 90 years. In this paper we inject still another possibility, one which in some ways conflicts with that of Wigglesworth. That two completely new and directly opposed ideas can be introduced at this stage, in view of the fact that hundreds of pages have already been written on the subject, attests to the inadequacy of existing reconstructions, and also to the reluctance of biologists to leave any of the pages of history blank when evidence is available, however meager and conflicting it might be. This seems to us a healthy attitude, and we present our ideas here principally in the hope that they will provide additional possibilities and renewed interest in the interpretation of evidence whenever it becomes available from any source.

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TIME OF WING ORIGIN IN INSECTS

Recent investigators seem agreed that the pterygotes, or winged and secondarily wingless insects, and the apterygotes, or primitively wingless insects, are derived from a common ancestor. The oldest hexapod fossil is a collembolan, or springtail, believed to be of Devonian age; other fossils of the soft-bodied Apterygota date only to the Triassic Period. The oldest fossils of winged insects date to Carboniferous, but all are fully winged, and several orders are represented, suggesting that wings may have originated considerably earlier. Recently, Rodendorf (1961) described a fossil from upper Devonian rocks which he believes to be a winged insect of a new order. The presumed wing appears from Rodendorf's illustrations and descriptions to be rather highly specialized. If this description is valid, and the age correctly determined, then some revisions in the antiquity of flight capacity in insects will be necessary. In any case, it seems clear that insects developed flight at least 50 million years before the vertebrates did, and before the insects themselves had burgeoned as a group. Less than one-half of one per cent of the nearly one million described modern insect species are primitively wingless. When wings originated, terrestrial insects would have been living with the ancient amphibians and reptiles, during a time when there were great forests of seed ferns and gymnosperms, presumably vast swampy regions, and no other aerial animals.

THE NATURE OF THE PTERYGOTE ANCESTOR

An overwhelming majority of investigators favor the suggestion that insects as a whole were derived from a terrestrial ancestor, and that among modern wingless arthropods the Thysanura bear the closest resemblance to the ancestor of winged insects (Jeannel, 1949; Carpenter, 1953; Ross, 1955; Lemche, 1940; Crampton, 1924). However, nearly all attempts to describe the ancestor of winged insects have resulted from efforts to reconstruct the origin of wings and flight; evidence from other sources is practically nil. There are no known modern insects or fossil insects with rudimentary wings or "half-way" developed flight, and the differences between modern and fossil apterygotes and pterygotes are considerable. Apterygotes are mostly small insects; the various pterygote orders anciently represented in the fossil record and characterized by constellations of apparently primitive features (Ephemeroptera, Odonata, and various orthopteroids) are mostly large insects. Some of these ancient orders have aquatic juveniles and aerial

adults; others are wholly surface-dwelling or wholly inhabitants of one sort of vegetation or another. For some of the extinct groups (e.g., Paleodictyoptera), no juveniles are known. We can say that the original winged insect probably had a simple kind of metamorphosis, but whether it was large or small, or where and how it lived, are questions which seem approachable at the present time chiefly on the basis of the probabilities that wings evolved from one or another kind of beginning and through one or another sequence of changes.

THE CURRENT PRINCIPAL THEORIES

Including Wigglesworth's recent hypothesis, most ideas concerning the origin of insect wings fall into three major categories, which we can discuss in the order of their appearance.

THE "FLYING FISH" HYPOTHESIS.—Oken (1831) considered insect wings to be homologues of the nymphal gills of a primitive insect with an aquatic juvenile—and in some modern Ephemeroptera, nymphal abdominal gills are indeed locomotory organs (Despax, 1949). However, there are apparently no notal thoracic gills in juveniles of modern insects, even though gills that are obviously of several different origins exist in the nymphs of Odonata, Ephemeroptera, and Plecoptera, and some thoracic gills are located beneath extensive notal flaps. The problems of transferring a juvenile apparatus adapted to function underwater into an adult structure adapted for locomotion in the air seem generally to have been by-passed by the proponents of this hypothesis. Flying fish give no good analogy, for insects are too small to break forcibly through the surface film in a comparable fashion. The only modern insects reported to use their wings to swim underwater are tiny hymenopteran parasites which enter the water by walking through the surface film on emergent plant stems or rocks (Lubbock, 1863). Such forms clearly represent secondary specialization. Perhaps not the least difficulty with Oken's hypothesis is the necessity of postulating an insect with an aquatic juvenile living in such a way as to render *rudimentary* flight in its adult selectively advantageous. Crampton (1916) gave a lengthy discussion casting doubt on ontogenetic and other evidence bearing on homology between wings and the known gills in insects; and Ross (1955) gave reasons for questioning the hypothesis that the first winged insects were aquatic.

THE "FLYING SQUIRREL" HYPOTHESIS.—Müller (1873) and others believed that insect wings arose as lateral outgrowths of the body wall with an early function as planing surfaces enabling a vegetation-inhabiting insect to glide from one plant or part of a plant to another.

Forbes (1943) and Ross (1955) have discussed this hypothesis in some detail. It may provide the right kind of ancestor for winged insects—a vegetation-inhabiting glider—but there is still the problem of starting notal flaps and getting them large enough to serve as gliding planes. The notum is produced laterally in many terrestrial arthropods, perhaps most strikingly in various crevice-dwellers (e.g., millipedes, silverfish, cockroaches); this may have happened many times in connection with flattening the body and rendering the animal more successful in avoiding certain kinds of predators—through providing lamellar armor, causing shadow reduction, enhancing leaf mimicry, or allowing more successful ensconcement in protective crevices. Becker (1958) has also discussed in some detail the possibility that lateral extensions of the notum may have originated (many times?), and even become rather elaborate, in association with reinforcement of the functioning of the large dorsoventral leg muscles. Such a tendency may well have been involved with the origin of insect wings. It restricts emphasis of the paranotal lobes to the thoracic segments, which of course bear the wings in insects; it can apply to a likely kind of ancestor of flying insects, an active, vegetation-inhabiting (perhaps arboreal, perhaps leaping) insect; and it could explain involvement of leg musculature in wing movement.

Wigglesworth's Hypothesis.—Wigglesworth (1963) has introduced the suggestion that wings arose in tiny, passively airborne insects. He believes that the provision of light cuticular expansions from the thorax in such insects would facilitate take-off; the existence or appearance of muscles which could twist such light planes would then increase take-off efficiency and afford some control during landing; and flapping muscles would next increase the efficiency of both take-off and landing. In this way very small steps toward the evolution of completely functional wings could at once have selective value. This novel hypothesis requires that the ancestral winged insect be a tiny species. But Ross (1955) and Pringle (1957) were of the opinion that the ancestral pterygote was a large species. It would seem that the tinier the insect, the less likely it would be that active flight could be advantageous, and the more drastic any initial change would have to be if it were functional in controlling flight. Wigglesworth cites the fact that aphids, which are often transported aerially for hundreds of miles, control their flight only during take-off and landing, but this example can also be used against his hypothesis if one suggests that these tiny insects have reduced their size beyond the level at which active control of flight is a reasonable possibility. Further, if Wigglesworth's hypo-

thesis is reasonable, one would expect to find repeated starts in this direction among tiny, passively aerial arthropods. Imperfect wings would seem to be better in all such animals than no wings at all, and imperfect "flight" in all of its developing stages would be better than completely passive aerial transport. In this respect, Wigglesworth's hypothesis differs from the others discussed here in which imperfect or rudimentary flight could frequently be disadvantageous among predator-susceptible, non-aerial species. Yet no instance of rudimentary wings in a modern, passively aerial arthropod has been cited. Finally, Wigglesworth's hypothesis does not account for the restriction of insect wings to the adult stage. Indeed, perhaps as often as not it is the juvenile arthropod that is passively transported through the air. In spite of these objections. this idea has many interesting aspects, and it provides useful orientation for investigators interested in the question of how wings and flight originated in insects (see below).

Some Dissenting Opinions.—As a matter of historical interest, it might be of value to record here some of the hypotheses that have deviated from those given above, and which have not gained wide acceptance for one reason or another. Lemche (1940, 1942) believed that wings as actual flying organs developed at least three times in insects, and that such modern insects as Grylloblattidae, female Zoraptera, and female Coleoptera (Lampyridae) may be primitively flightless. On the other hand, Handlirsch (1908), Tothill (1916), and Raw (1956) believed that even the Apterygota have lost their wings, although it is not always clear that these authors refer specifically to flying organs when they speak of wings. Various authors have suggested that winged insects were derived directly from annelid ancestors, and that their wings are modified parapodia (Walton, 1927; Raw, 1956). Others have suggested reasons for deriving insects from ancestors resembling Trilobita (Handlirsch, 1908), Crustacea (Hansen, 1893), Chilopoda (Tothill, 1916), and Onychophora (Versluys and Demoll, 1921). Jeannel (1949), Carpenter (1953), Ross (1955), and Raw (1956) discuss these various theories and most of their aspects pertinent to the present discussion.

MATING BEHAVIOR AND THE ORIGIN OF INSECT WINGS

With the exception of Wigglesworth's hypothesis, it is clear that the principal weak link in reconstructions of the beginnings of flight in insects involves the adaptive contexts in which notal flaps could begin and become extensive enough to be elaborated in a flight function. The nature of the insect involved is critical. It seems to us that the most

convincing sequences described so far have been those involving a fairly large, active, vegetation-inhabiting insect which developed a flattened body and extensive paranotal lobes in connection with (1) life in crevices, (2) the enhancement of locomotion, (3) leaf mimicry, (4) shadow reduction, (5) lateral armoring, or (6) some combination of these functional contexts. These characteristics could from the start have improved such an insect's overall ability to lead an arboreal adult existence, and could have led eventually to a rudimentary gliding function, perhaps similar to that secondarily present in the true katydid, *Pterophylla camellifolia* (Fabricius), an arboreal, leaping, flightless insect which spreads its leathery, convex forewings and glides or "parachutes" to a lower branch or to the ground when disturbed or dislodged. The advantage might initially have lain in increasing success in landing on lower perches without dropping all the way to the ground with each leap. Dropping to the ground, while obviously a selective advantage under certain conditions, can also place an arboreal insect at sufficient disadvantage that special orientation resulting in recovery of the original position can evolve in conjunction with the dropping behavior. Thus, Bradley (1962) has shown that aphids which drop to the ground upon the slightest disturbance orient immediately toward large, dark objects, and begin steady locomotion which replaces them in their original arboreal locations.

There is an interesting correlation between this hypothesis and that of Wigglesworth, for an active, arboreal insect which frequently leaps is in fact "passively aerial" during its leap, especially when it must drop all the way to the ground. Small notal flaps could, in this hypothetical, large, jumping ancestor as well as in Wigglesworth's tiny, aerial ancestor, be advantageous from the start in controlling both take-off and landing.

Beginning at a gliding or rudimentary flying stage reached by any combination of the above changes, one would need only to account for selective elaboration of the flight function. But some questions remain unanswered. If paranotal lobes became wings as a result of selection related to locomotion, or to predation in connection with any of the functions given above, then how is it that insect wings are restricted to the adults, and from the available indications always have been? The only exception is the brief subimago of the Ephemeroptera, which Ross (1955) suggests may represent retention of a primitive condition in which winged insects continued to molt throughout life as most of their apterygote relatives still do.

It is not difficult to understand the advantages of the dispersal function being restricted to the adults of insects as we see them today, or

even to the adult female in some cases. But, except in the case of Wigglesworth's hypothesis, dispersal could scarcely have been a major advantage in the *initial appearance* of flight capacity. Another question is whether paranotal flaps having any of the primitive functions mentioned above could have evolved into flying devices without the intervention of some other mode of selection. We suggest that there may have been intervening selective action, and that it could have been associated with the mating act.

The reproductive behavior of insects has apparently never been directly implicated in hypotheses concerning the evolutionary origin and development of wings, although there seems to be considerable evidence to suggest such a relationship. To begin generally, none of the primitively wingless insects is known to have a copulatory act in which the male and female genital openings are brought into apposition, or in which there is involved an aedeagus or male intromittent organ. But all winged or secondarily wingless insects do have direct copulation, except for such rare aberrations as some of the cimicid bugs in which a spermatophore is deposited on the female's body wall and dissolves its way into the body cavity (Khalifa, 1949; Ghilarov, 1958). Did a copulatory act appear in the ancestor of winged insects before, after, or during the time that wings were evolving? With regard to sexual behavior, the ancestor of the arthropods apparently made the original transition from aquatic to terrestrial life in essentially the same way as the vertebrates; while still living in an aquatic environment, it must have developed internal fertilization through transfer of a sperm sac or spermatophore, and then a desiccation-resistant egg with a relatively thick covering laid down by glands in the female's body. Today all insects have either a spermatophore or the traces of it, or else they have accessory glands believed to have evolved from spermatophore glands (Khalifa, 1949; Davey, 1960).

But when and how did a direct mating act evolve? Among the nonhexapod terrestrial arthropods and the primitively wingless insects, indirect methods of sperm transfer are diverse and bizarre. In at least one springtail insect (Collembola), the male is reported to insert a spermatophore into the female's vagina with its mouthparts (Lie-Patterson, 1900), while male spiders utilize a syringe-like device in the pedipalps (Bristowe and Locket, 1926; Locket, 1926; A. J. Alexander and Ewer, 1957; Levi, 1961). Some female millipedes and springtails pick up spermatophores deposited on the ground by the males and insert them into their own vaginas; various male scorpions, centipedes, springtails, and thysanurans maneuver their females in elaborate "dances" to effect the pickup of spermatophores or sperm droplets

they have deposited on the ground, on stalks, on threads, or on objects of different sorts (Spencer, 1930; Schaller, 1952; Stürm, 1956; A. J. Alexander, 1957; Klingel, 1960). With the exception of the Odonata (in which the mating act is aberrant, with the male first placing the sperm into a secondary transfer apparatus on the venter of his second and third abdominal segments and then transferring it directly to the female's genital opening), all primitive pterygote insects—Ephemeroptera, Plecoptera, and the orthopteroid orders—either mate with the female mounting upon the male's back or in a manner suggesting that they have descended from an ancestor that mated in this fashion. For example, in mayflies, the male seizes the female from below in flight; and in mantids, phasmids, grasshoppers, stoneflies, and termites, although the male either mounts the female or stands more or less beside her, he lowers his abdomen and reaches up from underneath to engage the genitalia (Chopard, 1938; Despax, 1949). In the thysanurans that have been studied, the male guides the female from the side, using his long caudal filaments and antennae, until her genitalia contact sperm droplets which he has just deposited on a thread that he is spinning out behind him (Spencer, 1930; Stürm, 1956). It is easy to see that only slight changes would be necessary to bring the male and female genitalia into direct apposition during this act, in which case, the male would be contacting the female from the side. One male thysanuran, *Nicoletia tergata* Mills, has an elaborate gland on its abdominal dorsum (Mills, 1940). The female remains unknown, and nothing is known of the behavior of this species other than that it lives in rodent burrows. However, specialized dorsal glands have arisen many times among the orthopteroids, and always in connection with the female mounting upon the male's back during copulation (Hancock, 1905; Fulton, 1931; Gurney, 1947; Roth and Willis, 1952). If winged insects arose from an ancestor resembling modern thysanurans, the mating act in *Nicoletia* may resemble the original copulatory act in the pterygote line.

In modern insects in which the male mounts the female in copulation, the male always utilizes some special grasping apparatus—his genitalia, his thoracic legs, or his cerci. Nevertheless, successful mating without some degree of cooperation by the female is rare, if it ever occurs. But copulation involving mounting by the female is quite a different proposition. Here the male is primarily a guider and signaller rather than a seizer and holder. He utilizes long, tactile, caudal filaments, and usually long antennae, to maneuver and guide the female; and he nearly always produces additional elaborate stimuli—chemical,

visual, tactile, auditory, or a combination—which induce the female to assume the copulatory position and remain there while the spermatophore is attached. The only exception known to us is a tiny cricket, *Cyrtoxipha columbiana* Caudell, which attracts the female into proximity with the usual stridulatory apparatus on the forewings, but then orients in front of the female, dashes backward under her, and attaches the spermatophore within a few seconds without any other evident special stimuli (Thomas J. Walker, pers. commun.). At the other end of the spectrum of variability represented by the available examples is a cricket, *Discoptila fragosoi* Bolivar, in which the male does not even attach the spermatophore, but simply holds it in place at the female's genital aperture for 15–90 minutes while it empties into her vagina (Boldyrev, 1928*a*). The female keeps the proper position because she is feeding at the secretions of two glands on the male's metanotum which he keeps exposed by holding the tiny gland-covering wing pads tilted forward over his pronotum. This example suggests an additional possibility for the initial appearance of hinged notal flaps; they could have evolved as covers over female-attracting dorsal glands.

Dorsal glands of five different origins are known in the family Gryllidae alone—single metanotal, paired metanotal, abdominal, tegminal, and tibial (Hancock, 1905; Boldyrev, 1928*a*; Fulton, 1930; Gabbutt, 1954; R. D. Alexander, 1962), and many others are known in other families with similar copulatory acts, e.g., Tettigoniidae, Gryllacrididae, Blattidae (Fulton, 1930; Gurney, 1947; Roth and Willis, 1952). In one cricket, *Hapithus agitator* Uhler, which does not have a courtship song but has two small metanotal glands (contrary to R. D. Alexander, 1962, Table 1), the male holds the wings in an unusual position during courtship and copulation. The mounting female is first attracted to the metanotal glands. Then, as the male attaches the spermatophore, she lifts her head and eats his wings. Eating of the wings was first noted by Blatchley (1891), and the entire act has now been observed several times by R. D. Alexander. A Russian katydid, *Bradyporus multituberculatus* Fischer-Waldheim, has tiny wings that are completely hidden under the pronotum. The male has no other obvious attractant, but the female bites at the oversized lip projecting backward from the pronotum until it bleeds, and then feeds on the blood while the male attaches the spermatophore (Boldyrev, 1928*b*). Thus, visual, auditory, and possibly tactile stimuli from the motion of the wings, chemical stimuli from glands of numerous separate origins on or under the wings, chemical stimuli directly from the wings and other notal lobes, and possibly even thoracic vibrations resulting from

wing motion and received as "substrate" vibrations through the tibial subgenual organs of a mounting female, all may serve as epigamic devices in various insects in which the female mounts the male in copulation. The 180° rotation of the male genitalia during development in many higher insects (e.g., Hymenoptera, Diptera) may in some instances reflect the reversal from a primitive female-above mating position. In any case, it is clear that arthropods have gone through a great many peculiar and complex evolutionary changes in the course of developing direct means of inseminating the female in terrestrial environments.

The above facts taken together strongly indicate that direct copulation (and perhaps also secondary aquatic life) appeared in insects at about the same time that wings originated; that most or all insects passed through a stage in which the copulatory act occurred with the female mounted on the male's back; and that therefore the male of the pterygote ancestor probably possessed dorsal female-attracting devices.

Paleodictyopteran fossils may bear importantly on the question of the origin of insect wings. These insects had large pronotal lobes in addition to their long, laterally-extended meso- and metathoracic wings. Their pronotal flaps have been interpreted either as vestigial adjuncts to a gliding function, or else as vestigial homologues of the meso- and metathoracic wings. But another interpretation is possible, and this is that the pronotal lobes in flying paleodictyopterans are actually more elaborate than they were in earlier members of the order which could only glide, or at least could not fly as well. If the wings in these insects had at some earlier time served as important attractants to the female during courtship and copulation, then it is possible that when the wings incidentally became functional in gliding or in helping the insect to make extended display or predator-escape "hops," and thus began to function specifically as flying organs, the pronotal flaps kept or took over the courtship function and became specifically elaborated in that connection. In fact, the pronotal flaps of paleodictyopterans—from published descriptions and figures of their fossil remains—give the impression of having been fleshy, articulated lobes better suited to an epigamic function than to a locomotory one. In some species the lobes were ornate. Their position, somewhat dorsal to the level of the wings, also suggests elaboration after evolution of the wings and the appearance of flight capacity. It is not impossible that the sometimes conspicuous paranotal lobes occurring on the abdominal segments of some paleodictyopterans with short caudal filaments were also functional mainly in orienting the female to or along the male's dorsum during the initial stages of the copulatory act—a function ac-

complished today by dorsal glands and long, tactile cerci in various orthopteroids.

An interesting point derives from Lemche's (1940, 1942) intensive study of the positions of developing wing pads in juvenile insects and his interpretations of their evolutionary significance. He concludes that in the ancestry of winged insects there were two different forms, one with rudimentary wings that extended backward and one with rudimentary wings that extended laterally. Because mayfly (Ephemeroptera) wings develop posteriorly but later move laterally and otherwise resemble those of the Odonata which seem to be derived from an ancestor in which the pads developed laterally, Lemche is forced to place the mayflies in still a third group. Whether or not acceptance of Lemche's polyphyletic origin of flying wings is indicated, his studies show that some striking complexities have occurred in wing positioning which may indeed reflect ancient differences among different evolutionary lines. If the hypothesis that early wings were heavily involved in mating behavior is correct, then it is apparent that shifts in positions and manners of development could have taken place on a considerable scale in this context, and perhaps earlier in the evolution of wings than other authors would have such changes occurring, though probably not as early as Lemche would have them occurring. Different lines of evolutionary change could thus have been initiated that would be difficult to understand on the basis of modification of the flying function alone. It is not difficult to imagine, for instance, that the position of wings that functioned during courtship and mating might be greatly influenced by whether they were serving as tactile, visual, or chemical devices, or, on the other hand, as covers for regions or glands that were chemically attractive to the female; or whether they were serving as pre-mating attractants or as devices that would keep the female in position on the male's back during the actual process of insemination. The wings of modern insects which function differently in these regards are held in different positions. Wings of *Gryllus* function in acoustical courtship and are lowered during courtship and mating; those of *Oecanthus* function acoustically and expose dorsal secretions, and they are held vertically during courtship and mating; wings of *Hapithus* expose secretions involved in causing the female to mount, then the wings are eaten by the female while they are held at approximately 60° with the male's body during mating; those of the mayfly are held laterally and somewhat dorsally during both flight and mating, and it is quite likely that they function as guides for the male or the female or both during assumption of the copulatory position.

Although it has been continually emphasized that the mayflies are

probably more similar to the earliest winged insects than are any other living winged insects, we should not forget that some of the present traits of Ephemeroptera—mating in flight, and short-lived, non-feeding, completely aerial adults, for example—are specializations that were probably developed only after flight had been evolved to a rather high degree and should not be considered causes of the evolution of flight. Even the aquatic juvenile could represent a specialization following the evolution of flight ability in the adults, although there does not now seem to be any way of determining whether or not this is so.

DISCUSSION

We have offered the suggestion that the pterygote ancestor was an insect with a terrestrial adult which mated either on the soil surface or on vegetation. The possibility of a vegetation-inhabiting ancestor is demonstrated by the true katydid, a secondarily flightless insect which is both arboreal and saltatorial, and in which the female mounts the male in copulation, and the same set of thoracic appendages (fore-wings) has been elaborated in a gliding function as well as in mating functions (stridulation, and lifting during copulation to expose dorsal areas apparently chemically attractive to the female). On the other hand, if subsequent evidence makes it seem more likely that flight arose in a surface-dwelling adult, then the band-winged grasshoppers (Oedipodinae) demonstrate that in non-arboreal insects, short flights begun with a leap can be specialized in connection with mating behavior (flight wing noises and display of brightly colored underwings).

Hinged notal extensions remotely similar to insect wings have evolved in one other branch of the Arthropoda, the so-called "pteromorph" mites (Acarina: Oribatei: Pterogasterina). Woodring (1962) recently discussed the evolution of this group and possible parallels between the evolution of the notal extensions of oribatid mites and the wings of insects. The primary function of oribatid pteromorphs is presumed to be protective because of the armoring effect produced by their depression along the sides of the body. Woodring suggests that a similar function may have occurred during evolution of insect wings, and that this could account for development of musculature and early extension of the flaps. Along with Grant (1945), he emphasizes the likelihood of incompatibility between gliding and flapping flight, and believes that "it would be easier for a hinge-winged (hence muscled), gliding form to evolve towards a flying form than for a nonhinge-winged gliding form to develop hinges and muscles in the process of evolving toward flight." However, there seems to be no evidence of

close similarity between protective mite "wings" and the present or past nature or functions of insect wings.

Although there is no good reason to believe that mite pteromorphs have ever been directly involved in mating behavior, there is evidence to show that some other external characters of mites may be closely related to courtship or copulation. According to Andre (1949), Mitchell (1957), Lipovsky, Byers, and Kardos (1957), and others, different mites exhibit either direct copulation or indirect spermatophore transfer, much as the various insects do. Among the mites with a direct copulatory act, different positions are assumed, including several variations of a female-above position. Males in some such species have greatly enlarged and specialized hind legs which are directed dorsally and posteriorly and hold the female during copulation (Andre, 1949, fig. 654). This is somewhat similar to the way that the males of some insects (Mecoptera) use peculiar, tong-like wings to hold the female in a dorsal position during mating (Cooper, 1940).

Aside from paranotal flaps, the elaborate dorsal setae of some mites seem very likely to have been modified in connection with mating behavior, although we have found no record of them being discussed in this connection. Andre (1949), for example, presents a color plate (plate VI, between pp. 858 and 859) showing male, female, and immature of *Oustaletia pegasus* Tnt., a bird parasite. The male has great dorso-lateral and posterior wing-like plumes which together form an open channel along his dorsum, while the female has an armor-like central row of posteriorly projecting enlarged dorsal setae. These structures strongly suggest that this species mates with the female on the male's back, and it is difficult to believe that the elaborate setae of the male, which superficially resemble wings in both position and shape, are in no way involved in mating behavior.

It is surprising that apparently no one has implicated mating behavior in the elaboration of vertebrate wings. In this connection, Dr. Ernst Mayr has conveyed to us his belief that the feathers of birds may have arisen first as a male sexual display character, and become incorporated only secondarily into the wings when the anterior limb was converted into a flight structure. He believes that the wings of most other flying or gliding vertebrates have most probably developed from a patagium. Schmidt (1935) and Hairston (1957) indicate that the rib-supported, wing-like folds of flank skin in the so-called "flying lizards" (*Draco* spp.) may be as important in courtship and territorial display as in escape from predators, and it seems quite possible that

these and many other bizarre dorsal and lateral growths among modern and extinct reptiles—the "sails" of *Edaphosaurus* and *Dimetrodon,* for example—were elaborated principally as epigamic display structures.

SUMMARY AND CONCLUSIONS

The wings of insects arose as flaps from the thoracic notum, and they probably served first in a capacity having nothing to do with flight. Previous authors have suggested that notal flaps could have originated as gills or gill covers in aquatic insects; as lamellar armor or otherwise defensive devices, or in connection with strengthening the thoracic leg muscles in large, terrestrial insects; and as controlling devices during take-off and landing in tiny, passively aerial insects. The new hypothesis offered here is in general that between the first notal extension, whatever its function, and the development of true flying wings, there was a time when notal flaps were elaborated as organs of epigamic display. As subsidiary possibilities, we may mention that the flaps could early have functioned (1) as covers for some dorsal, female-attracting glands, or (2) in controlling take-off and landing in large, vegetation-inhabiting insects. Evidence for these hypotheses lies principally with the restriction of wings to the adult stage, the fact that all pterygote insects give indications of having passed through a stage in which the female mounted the male in copulation, the probable timing of the origin of the copulatory act in the hexapod lineage, the position of insect wings on the body, and the evolution of diverse, elaborate structures in modern insects (and mites) which mediate mating acts that occur with the female in the superior position. An "advertisement" function in courtship or territorial display could conceivably have accounted not only for a considerable part of the elaboration of wing precursors, but also for their initial movement and articulation as well. Once flying ability had acquired significance in some context other than mating—possibly during a gliding stage—it would not have been difficult to transfer to the female an apparatus already possessed by the male. It is also possible that structures and activities leading to flight could have developed concomitantly in both sexes, for example, as species-specific recognition characters.

The questions brought up by this paper have by no means all been answered with a reasonable degree of certainty. It is clear from the diagram in Figure 1 that several explanations of wing evolution are still possible, but some of them are very weak. Surely some alternatives can be eliminated, and others rendered more likely, with evidence

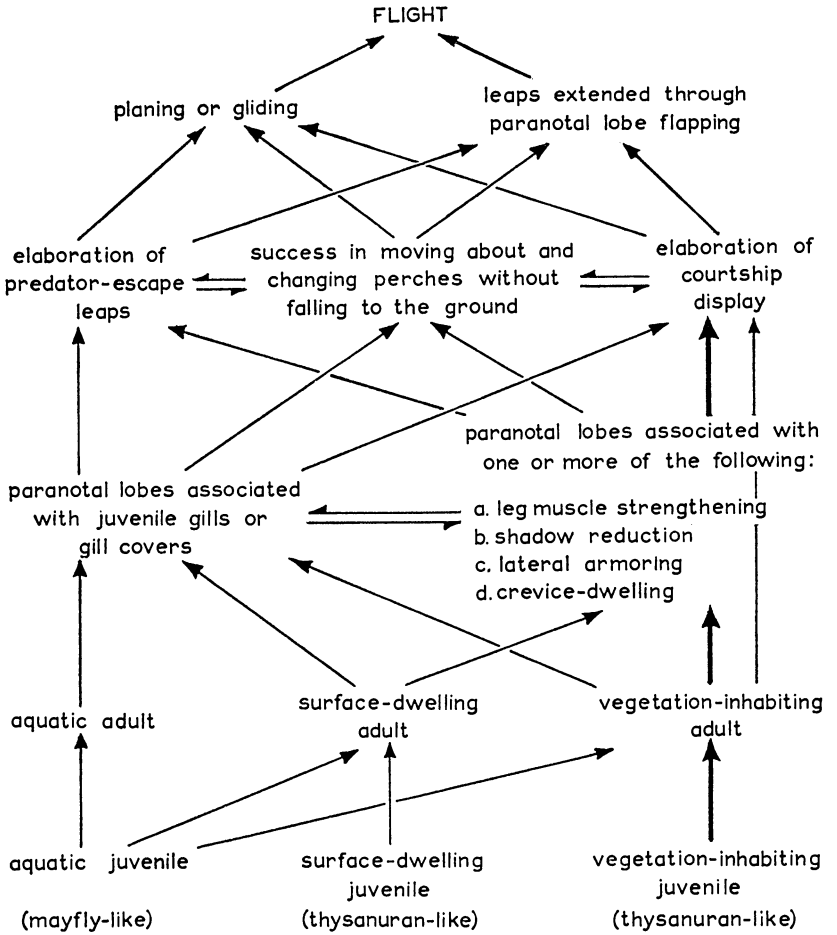

FIG. 1. Diagrammatic illustration of some of the possible pathways of evolutionary change in the origin of flight in insects. Heavy arrows indicate a sequence we believe to be most likely. This diagram was completed prior to our reading of Wigglesworth's (1963) hypothesis. Since his ideas would represent a completely separate sequence, we did not revise it to include them.

that will become available in the future. The present re-synthesis of the available information, and modification of the existing hypotheses, may lend new orientation to the interpretation of fossil evidence and other kinds of materials, and it emphasizes the potential value of comparative behavioral studies in the vast number of arthropod genera whose behavior is still almost completely unknown.

ACKNOWLEDGMENTS

We are indebted to Drs. Norman E. Hartweg, Theodore H. Hubbell, and Thomas E. Moore of the University of Michigan Museum of Zoology, Dr. L. J. Stannard of the Illinois Natural History Survey, and Dr. E. O. Wilson of Harvard University, for helpful criticism of the manuscript. Dr. Stannard pointed out to us the possibility of leaf mimicry in early development of tergal flaps and the correlation between emergence of specialized plant leaves and the probable time of origin of insect wings.

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Accepted for publication April 2, 1963