the life history in breeding cages. Dr. Howard thought that Mr. Simpson's method of observation and record was most surely calculated to furnish the data for correct conclusions.

—The final paper of the evening was by Prof. Cook, and entitled:

## THE EARWIG'S FORCEPS AND THE PHYLOGENY OF INSECTS.

By O. F. Cook.

The earwigs are a group of tropical insects with very few representatives in temperate regions. But in spite of their retiring habits they have received a considerable amount of popular attention, because of the fear inspired by the rather formidable pair of forceps carried at the end of the body. Entomologists know, however, that the creatures are quite harmless, and that their forceps are not only free from any poison glands, but are not sufficiently strong to make a wound or puncture. In fact, no adequate explanation of the function of the forceps seems to exist, as evidenced by the following summary of the scientific knowledge of the subject by Dr. Sharp, the eminent entomologist of the British Museum.

"The pair of forceps with which the body is armed at its extremity forms another character almost peculiar to the earwigs, but which exists in the genus *Japyx* of the Thysanura. These forceps vary much in the different genera of the family; they sometimes attain a large size and assume very extraordinary and distorted shapes. They are occasionally used by the insects as a means of completing the process of packing up the wings, but in many species it is not probable that they can be used for this purpose, because their great size and peculiarly distorted forms render them unsuitable for assisting in a delicate process of arrangement; they are, too, always present in the wingless forms of the family. Their importance to the creature is at present quite obscure; we can only compare them with the horns of lamellicorn Coleoptera, which have hitherto proved inexplicable, as far as utility is concerned. No doubt the calipers of the earwigs give them an imposing appearance, and it may be of some little advantage on this account; they are not known to be used as offensive instruments for fighting, but they are occasionally brought into play for purposes of defence, the creatures using them for the infliction of nips, which, however, are by no means of a formidable character."*

For at least one member of this group this deficiency of knowledge can be supplied by the fact that an earwig supposed to be

* The Cambridge Natural History, V, p. 208, 1895.

*Labia minor* Scudder, common in the vicinity of Washington, uses its forceps to spread its wings, and is apparently unable to resort to flight without the assistance of its caudal armature.

It is well known to entomologists that the hind wings of the earwig differ from those of all other insects, except those of the Staphylinid beetles, in being folded transversely to fit under the short anterior wings, which serve merely as protective covers. The method of folding is, however, entirely different in the two groups, and the suggestion of the above quotation that the earwiguses the forceps to fold the wings seem to be quite erroneous. It was probably borrowed by analogy from the beetles, where the flexible abdomen is used, as it were, to tuck the wings under their covers. The wings of the Staphylinidæ are still expanded when the insect alights, and are sometimes allowed to remain so when neglected through fright or annoyance.

With the earwig, on the contrary, the closing of the wings is instantaneous and apparently quite automatic; when the insect alights its wings are completely folded, and it runs away without the necessity of any of the preliminary contortions of the Staphylinidæ. Moreover, unlike the beetle, the earwig does not open its wings readily or when running. The operation is obviously a special effort which requires it to stand still and exert its undivided attention for a very appreciable interval. The wing covers and wings are soon raised from the body, but the wings do not unfold until, by repeated quick upward movements of the recurved abdomen and forceps they are, as it were, combed out and spread for flight. Occasionally an earwig seems to lose the power of keeping the wings open, and repeatedly falls down after short flights of an inch or two, though apparently making efforts at longer journeys. Instead of direct flights, they often rise and continue to gyrate in a spiral about two inches in diameter.

It is, of course, possible that this observation would not apply to all the winged earwigs, and, to judge from the past, much time will be needed for its verification in the different families and genera of the group. That the present use of the forceps remained so long unnoticed is probably to be explained by the fact that the earwigs, like the termites, are nocturnal or twilight insects, and when disturbed in the daytime never attempt to use their wings, but run for shelter and concealment in the dark. The insects which were seen to fly had been attracted to a light in the evening, and there also flight seemed to be undertaken only when the creatures felt themselves at leisure. When annoyed or frightened they attempted only to run away the faster. Several genera of earwigs, including *Apachya*, collected under similar circum stances in Liberia, were also seen to alight with their wings already folded, and to bend their abdomens while resuming flight, though the nature and object of the movements were not then ap-

preciated or noted in detail. The complexity of the wingfold is such, however, that the need of an accessory organ like the forceps appears by no means improbable, and in the absence of any other suggestion of general pertinence, it seems not unwarranted to proceed on the assumption that the primary use of the forceps of the earwig is the unfolding of the wings.

It is, of course, to be expected that such organs as the forceps would be utilized in other ways, though the failure of entomologists to discover such secondary functions may be taken as an indication that no very extensive adaptation has taken place. The most that can be said at present is that both in the earwig and in Japyx the long, slender hairs with which the forceps are sparingly clothed are an indication that the tactile sensibility residing in the stylets of many insects is at least partially retained. In some genera the forceps have become enlarged and thickened to an extent strongly suggestive of a defensive use, and it is of further interest to note that such forms are often wingless, and that the broadening and thickening of the abdomen tends to diminish the flexibility which is retained by the more slender form and laxer skeletal structure of the winged genera. The unusually broad abdomen of the winged African genus *Apachya* is an exception to this rule, but here flexibility is provided for by the extreme thinness of this part of the body, while the forceps are so peculiar as to suggest the existence of some unique adaptation. There also exist winged species with robust bodies and strong forceps, but, like many beetles, these may make no use of their wings. Indeed, it is easy to understand the evident tendency toward the abandonment of so specialized and difficult, and at the same time so relatively unnecessary an activity as flying seems to be among the earwigs. With the earwigs, as with the termites, the wings probably serve the single important purpose of cross-fertilization, interbreeding, or panmixia, which conduces at once to organic vigor and to evolutionary progress. But owing to their more active habits and their freedom from social organization and caste specialization, the power of flight is of much less vital importance to the earwigs than to the termites, and although the latter use their wings for but a single flight all sexual individuals are winged, while many genera of earwigs long since abandoned flight altogether.

The existence of so many wingless earwigs is not, however, an argument against the use of the forceps with the wings, nor against the adequacy of such an explanation of the evolutionary origin and universal presence of the forceps in this group of insects. Such an objection could be maintained only on the theory that the ancestral earwig was wingless, and that wings have been independently developed by different genera of earwigs, a position which nobody is likely to maintain. It is appreciated, however,

that the failure of any of the wingless earwigs to lose the forceps is not in accord with commonly accepted evolutionary theories. Instead of dropping the forceps with the wings, the caudal appendages have, in some cases, apparently increased in size, and have certainly continued to differentiate in form, attaining, for example, a marked asymmetry in the wingless genus *Anisolabis*, a condition which could not possibly have a functional significance in connection with the wings, and in all probability has none in any other relation. The continued presence of the forceps in the wingless earwigs is, moreover, paralleled as an evolutionary phenomenon by the equally useless multiplicity of form which appears in the forceps of the winged genera. The function here ascribed to the organs in question renders it highly improbable that there is the slightest use in the differences of form, size, and armature of the forceps, and the great variability of these characters also forbids the supposition that any definitely specialized uses remain unknown. Both sexes of *Labia minor* use their forceps in the same manner, though the form of the apparatus is very different, and it is nearly twice as long in the male as in the female. This is probably one of the endlessly numerous secondary sexual differences having no direct use, but perhaps serving an important purpose in contributing to the diversity which many organisms maintain inside specific lines. The general maintenance of a direct proportion between the length of the abdomen and the length of the forceps* supports the view that natural selection has tended merely to keep the forceps long enough to reach back to the wings.

The field of biology abounds, however, in similar phenomena which appear to be anomalous and mysterious when viewed from exclusively selectional or static theories of evolution, but which it seems preferable to interpret as examples of a general law of biological change for its own sake, as it were, and independent of natural selection.†

As accessories of the organs of flight the forceps are, of course, to be looked upon as an adaptation, but from what? Presumably from the jointed stylets to be found in so many groups, but more particularly from such as those of the peculiar insect described by Westwood, under the name *Dyscritina*.‡ but subsequently reported to be the larva of an earwig. Dyscritina, which the writer has observed and collected in Liberia, may be said to com-

* In a few cases where slender species have short forceps, the abdomen seems to be unusually flexible, but in general the long forceps go with the long bodies.

† A Kinetic Theory of Evolution, Science, N. S., XIII. No. 338, pp. 969–978, June 21, 1901.

‡ Trans. Ent. Soc. London, 1881, p. 601. Pl. xxii, Figs. 1–1i.

bine the habits of the earwigs with those of the true Thysanura. It lives among vegetable debris in very moist places, is extremely quick and agile in its movements, is very soft and delicate in texture, and is provided with a pair of long, many-jointed stylets instead of the forceps of the adult earwig. Curiously enough, these are exactly the differences which obtain between Japyx, the only other insect with forceps like the earwig, and the smaller and more thysanuroid analogue of *Campodea* also found in Liberia and described before this Society in 1899, under the name *Projapyx*.* Recently Projapyx has been found to be not uncommon in Porto Rico, and seems always to occur in the same localities as the Porto Rican species of Japyx, that is, in all sorts of situations from moist valleys to the tops of dry limestone hills.

But if Projapyx is really the larva of Japyx, students of the temperate species have failed of their full duty, or else we have found repeated in this order† the strange conditions of the earwigs where some species have a larval stage and a metamorphosis which have been suppressed in the others.

It is realized that this reasoning reverses, for the present case, at least, the opinion held by Lubbock and others that the larval stages of insects are derivative and adaptative, not ancestral and primitive. No reason is, however, apparent why one of these opinions should exclude the other, and in the present instance it seems obvious that from the standpoint of hexapod structure Dyscritina is much less specialized than the adult earwig, or than the larva of the Hymenoptera or Lepidoptera.

If, instead of holding that the Dyscritina stage of the earwig is an adaptation, we interpret it as a more primitive condition, it will be necessary to apply the same reasoning to the orthopterous groups to which the earwigs have been thought to be closely allied. Most of the cockroaches, like most of the earwigs, have no pronounced metamorphosis, but in several genera there is a transformation in both sexes, while in others only the males reach the winged condition. Metamorphosis is more accentuated among the cockroaches than among the remaining orders of Orthoptera, so that the current opinion that these insects are primitive because they have no metamorphoses is self-contradictory.

Having thus emancipated ourselves from the notion that the cockroaches represent the primitive insect type, it will be easier to appreciate at its proper value the long-obvious probability

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* Proc. Ent. Soc. Washington, iv. 222, 1899.

† A separate order Dicellura was established for Japyx in 1896, for the reason that it seemed more remote from the true Thysanura than the latter are from the Orthoptera. See Brandtia, p. 49, July 30, 1896; also Proc. Ent. Soc. Washington, iv, 222, 1899.

that the ancestral distinction belongs to the so-called neuropterous orders with aquatic larvæ and complete metamorphoses. Dyscritina as the larva of an earwig, and Projapyx as the larva of Japyx, bring the orthopterous series closer to the aquatic larvæ of the Neuroptera, with their many-jointed stylets, and thus permit us to think of the archetypal insect as a creature with metamorphosis and with wings instead of beginning with a thysanuran ancestor and being compelled to imagine the wings as appearing "independently at several points" as maintained by Professor Smith.*

For the correctness of this view, that the neuropterous orders with aquatic larvæ are the more primitive,† a large amount of evidence might be brought together, but perhaps the most conspicuous advantage of this standpoint lies in the fact that it permits the suggestion of an origin and method of development for the insect wing, which can scarcely be accounted for by any rational evolutionary theory beginning with the assumption that the first insects were land animals.

The wings of the birds, pterodactyls, bats, fishes, and other flying animals, are known to be modifications of organs used for locomotion in water or on land, but we have been contented to assume that the wings of insects were made, so to speak, from whole cloth, and have failed to associate them as the homological equivalents and derivatives of older structures used for purposes other than flight.

Kinetic evolution views as normal the progressive change of any particular part, but would not prearrange and carry forward the complex and delicate adjustments of structure and function necessary to the perfection of such organs as wings, since, except for flying, wings are about as useless structures for terrestrial insects as could well be imagined, and some representatives of nearly all the orders have abandoned them.

But if the discussion be transferred to the water, we have, so to speak, much clearer sailing. Fins too small for flying are still very useful to fish, and a gradual and natural increase of size of swimming organs to the point where they can be used for flight is illustrated by the analogy of the flying fishes.‡

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*An Essay on the Classification of Insects, Science, N. S., v, p. 671, April 30, 1897.

†The copulatory apparatus of the Odonata, located on the second segment of the abdomen, is paralleled only in the Diplopoda. The paired genital openings of the Ephemerida and the moulting of the insect in adult form are, if possible, even more primitive features.

‡Some of the so-called flying fish merely soar for short distances on their expanded wings, but others are capable of true flight, not by flapping their wings like birds, but by keeping them in a state of very rapid vibra

The lack of means of aerial existence and of locomotion on land has kept the fish from terrestrial conquests, but aquatic insects are not thus restricted, and thousands of species, including members of many different orders, are still able to make the ancestral substitution of a terrestrial for an aquatic habitat. Many also remain in the water as adults, and use their wings for swimming. Some of the May-flies descend into the water to lay their eggs, and in the genus *Pteronarcys* the adult winged insect has external gills. The most conspicuous suggestion for the formation of wings from gills is, perhaps, to be found in the larvæ of the May-flies, where the gills have become subdorsal and the tracheæ which, in other groups, hang in brush-like clusters, are spread out instead as veins of delicate, leaf-like membranes, and even arranged in a manner strongly suggestive of the patterns of the wings of some adult insects of other groups. The utilization of the anterior pairs of such lamillar gills as swimming organs, and their subsequent further specialization as wings, is thus a supposition requiring no abrupt or improbable change of structure or function, and affords a rational explanation of organs otherwise as mysterious morphologically as the wings of angels.

So much for the argument afforded by the winged and wingless earwigs, and the similarity of the jointed stylets of the earwig larvæ to those of Projapyx and Campodea. Shortly after writing this sketch of phylogenetic possibilities, I received from Dr. Filippo Silvestri,* of Bevagna, Italy, a paper in which my meagre account of the anatomy of the African Projapyx is greatly extended by observations on a South American species. Dr. Silvestri not only agrees with me that Projapyx is the most primitive of insects, but he holds in addition that it proves the descent of the insects from the diplopods, because he finds that the jointed stylets are spinning organs homologous with those of *Scolopendrella* and with those of the diplopod orders Cœlocheta† and Monocheta. But if Projapyx is the larva of Japyx instead of a mature insect, Dr. Silvestri's reasoning must be reversed, and we should prepare ourselves to believe that the Symphyla, Diplopoda and Pauropoda do not represent the ancestors of the hex-

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tion through a small arc, like the insects. The distances traversed are too great, and the rate of speed too slow and too uniform to be explained by the momentum with which the fish leaves the water. This conclusion is the result of many excellent opportunities of observation within the last ten years, principally in the Cape Verde region of the Atlantic. The objection of some ichthyologists that the flying fish is not so constructed as to be able to vibrate its fins in the air would also render these organs useless in the water.

* Boll. Mus. Zool. Anat. Comp. Univ. Torino, No. 399, Sept. 12, 1901.

† Brandtia, p. 41, 1896.

apods, but are, as it were, larviform off-shoots from the insect phylum. In other words, we may compare the diplopods with caterpillars and other larvæ, and may seriously undertake the study necessary to determine the reality of what have been supposed to be merely superficial similarities, such as the form of the cephalic sclerites, the barbed hairs and the repugnatorial pores. *Polyxenus* looks enough like a caterpillar, and its large fossil relative *Palæocampa* would have been even more strongly suggestive of such an affinity.* Moreover, a hexapod origin for the Diplopoda would explain the fact that the diplopod larvæ are hatched with the six anterior legs, the remaining pairs being attached to rings intercalated behind the genital segment. The anamorphous Chilopoda are hatched with seven pairs of legs, but the others are added by intercalation in front of the genital segment, which thus appears near the posterior end of the body in the one group and near the anterior in the other.

In this way it is possible to bridge the chasm which seemed to so profoundly separate the Progoneata (Diplopoda, Symphyla, and Pauropoda) from the Opisthogoneata (Hexapoda and Chilo-

* The barbed hairs of the larvæ of the Merocheta, and the bristles of the Cœlocheta, Monocheta and Colobognatha support the view that the soft-bodied, hairy Polyxenus is the most primitive of existing diplopod types. It may also be said that the skeletons of the different orders of Diplopoda are too diverse to be rationally explained by descent from a single hard-bodied type. In the Merocheta the segmental rings are solid and complete, without even traces of sutures to represent pleural or ventral plates. In the Cœlocheta, Monocheta, and Colobognatha the ventral plates are free; in the Diplocheta, Zygocheta, and Anocheta they are adnate, but are distinct by sutures. The pleuræ are free in the Oniscomorpha and Limacomorpha and in the Siphonotidæ; adnate in the Polyzonidæ and remaining Colobognatha, and in the Monocheta and Anocheta; no traces of pleural elements have been reported in the Diplocheta, Zygocheta, Cœlocheta and Merocheta. Finally, in the order Anocheta, the dorsal part of the segmental ring is composed of three transverse bands, a condition perhaps paralleled only in the larvæ of the saw-flies. From the entomological standpoint these differences would be thought very grave; indeed, they may be said to be altogether too grave for explanation by evolutionary changes in parts already hardened. If, however, we think of them as independent acquisitions of firm armor by soft-skinned animals we have ample analogies in other groups. This interpretation does not, of course, decrease the actual diversity, but it enables us to credit the evidence of the otherwise great similarity of structure and function among the Diplopoda. It permits Polyxenus to be more closely associated with the other Diplopoda, and brings the Diplopoda, as a group, closer to the Symphyla and to the Hexapoda.

poda). That there could be any derivative relationship between a group of animals with the reproductive system opening in the anterior part of the body (Progoneata) and others with the reverse arrangement (Opisthogoneata) seemed impossible, unless the common origin were traced back to worms with unspecialized reproductive segments. Should the present suggestion prove to have a foundation in fact, we shall have firmer ground for believing that the insects and the four classes commonly grouped as "Myriapods" do in reality constitute a natural assemblage.*

Nor do the possibilities of integration end here, since the association of the Progoneata with the insects as derivatives of an originally aquatic group reopens the whole question of their affinities with the Crustacea and Arachnida, and may result in the rehabilitation of the Arthropoda as a natural phylum or primary division of the animal kingdom.

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The paper was discussed briefly by Messrs. Simpson, Gill and Stiles. Mr. Simpson said that Prof. Comstock had given serious consideration to the theory that the primitive and original insects were aquatic and winged, but had finally abandoned it as untenable. He had noted that the tracheal gills of certain Mayflies are of almost the same pattern as the wing veins. This similarity, however, he had found to be accidental. Dr. Gill said he thought that there was no ground for believing that insects were derived from myriapods. There was a possibility, however, that they had sprung from an entomostracan type, though this was merely an hypothesis. Insects may have existed in palæozoic times, but there was no evidence of it. He maintained that flying-fish do not have a true flight, but that their enormously enlarged pectoral fins serve merely as parachutes for their sustentation in the air until the initial momentum of the fish leaving the water is exhausted.

Prof. Cook, however, maintained that certain of the flying-fish really progress through the air by a rapid vibration of the wings. He spoke of the resemblance of some geologic Crustacea to the larvæ of certain species of cockroaches as of interest and suggestive.

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* For this the name Labrata was proposed in 1896 (Brandtia, p. 30). The Labrata were deemed co-ordinate with the Branchiata (Arachnida and Crustacea) and the Malacopoda (Peripatus).