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ART. XXVII.—*On the Diptera or two-winged Insects of the Amber-fauna. (Ueber die Diptern-fauna des Bernsteins):* a lecture by Director LÆW, at the meeting of the German Naturalists in Königsberg, in 1861.¹

OF all the organic remains of former geological periods, those enclosed in amber are the most remarkable for their state of preservation, which is such that they admit of the most complete investigation. While under other conditions smaller and more delicate animal organisms have either almost or quite disappeared, in this case it is the very reverse, and hence the amber-fauna has an extraordinary richness in species, so that both for its beauty and abundance it invites to an investigation which promises the most interesting results. The objects for such investigation however are so various, that a division of labor is required. Induced by my deceased friend, Behrendt, I commenced the study of the Diptera preserved in amber nearly seventeen years since, and have continued it, not without unavoidable interruptions, up to the present time. A rich supply of material for this study has been supplied from various sources, and with a liberality which remained undiminished, in spite of the unexpected length of time required by the investigation. The principal por-

¹ We owe this translation of Director Læw's interesting Lecture on the Amber-fauna Diptera to Baron OSTEN SACKEN, so well known for his important contributions to the study of American entomology. The many points of interest which this lecture affords to American naturalists will render the translation peculiarly acceptable to English readers who have not access to the original. The author himself has kindly furnished the notes, containing lists of species common to Europe and North America, and which, not being found in the original, are here published for the first time.—(*Note by the Editor.*)

tion of this supply is the entire Behrendt collection of *Diptera* in amber, to which that of Aycke has been added; also rich contributions from the collection of H. Menge, of Danzig, from that of the Physico-economical Society of Königsberg, as well as from the Thomas collection in the Royal Mineralogical Museum at Berlin, without special mention of valuable contributions from individual collectors, who have with praiseworthy liberality sought to advance the aims of science.

The investigation of this rich supply of material has, up to this time, made known about 850 species of *Diptera* in amber, and these all belong to the division of the *Diptera proboscidea*, while, so far, not a single species of the *Diptera eproboscidea* has been found to occur. Of these 850 species, however, there are only 656 in so complete a state of preservation that their specific characters can be determined with absolute certainty. These are distributed over 101 genera, of which 50, with 395 species, belong to the *Diptera nemocera*, and 51, with 261 species, to the *Diptera brachycera*.

In the case of the latter, the chemical decomposition of their larger bodies, the more vigorous resistance which they have made to their entombment in the yet soft resin, the slighter development of their antennæ and legs, (organs which furnish such important characters for the ready distinction of the *Diptera nemocera*,) and still more, the few characteristic points in the neururation of the wings in most of them, for the distinction of species, of genera, and even of families, all conspire to render the proportion of fragments quite useless for exact determination much greater among the *Diptera brachycera* than among the *Diptera nemocera*. If such specimens could be turned to account, the above mentioned proportion of species would be greatly increased on the side of the *Diptera brachycera*.

The 50 genera of *Diptera nemocera* are distributed over all the families which have been formed for the living species, with the single exception of the small family of the *Blepharoceridæ*, if this is not united with that of the *Simulidæ*. The family of the *Mycetophilidæ* is the richest of all the others, both in species and in numbers; the family of the *Culicidæ* is the poorest.

From what has been said above, as to the frequently imperfect preservation of the *Diptera brachycera*, it can easily be understood that for many of the species found in amber, a definite place in the systematic arrangement can be assigned only with great difficulty. This is true especially for those families which have generally been included under the name of *Muscaridæ*, that is, all of the families and genera which Meigen, in his arrangement, places after the genus *Myopa*. For this reason, it is absolutely necessary to distinguish those families of the *Diptera brachycera* whose occurrence in amber is beyond a doubt, from those which are more or less doubtful. The families which are

now known certainly to occur in amber, are the following seventeen: *Xylophagidæ*, *Tabanidæ*, *Leptidæ*, *Cyrtidæ*, *Asilidæ*, *Therewidæ*, *Bombylidæ*, *Syrphidæ*, *Pipunculidæ*, *Hybotidæ*, *Empidæ*, *Tachydromidæ*, *Dolichopodidæ*, *Helomyzidæ*, *Micropezidæ*, *Diopsidæ* and *Phoridæ*. The families whose existence in amber is tolerably well established, are the following ten: *Myopidæ*, *Tachinidæ*, *Dexidæ*, *Muscidæ*, *Anthomyidæ*, *Sciomyzidæ*, *Sapromyzidæ*, *Ephydrinidæ*, *Drosophilidæ* and *Oscinidæ*. As families, which seem not to be represented in amber, we may name six: the *Sarcophagidæ*, *Lonchæidæ*, *Heteroneuridæ*, *Opomyzidæ*, *Piophilidæ*, and *Geomyzidæ*. Finally, there are eighteen families of which it is perfectly certain that not a single species has been found in amber, namely: *Stratiomyidæ*, *Acanthomeridæ*, *Mydasidæ*, *Hirmoneuridæ*, *Scenopinidæ*, *Platypezidæ*, *Lonchopteridæ*, *Æstridæ*, *Cordyluridæ*, *Psilidæ*, *Ortalidæ*, *Trypetidæ*, *Phycodromidæ*, *Sepsidæ*, *Agromyzidæ*, *Phytomyzidæ*, *Asteidæ* and *Borboridæ*. Of the families above named, the *Dolichopodidæ* far exceed all the others both in the number of species and of individuals; next to this come the *Empidæ*, as far as the species are concerned, but the number of individuals is far less. The families represented by only one species, found only once, or at most twice, are the *Tabanidæ*, *Bombylidæ*, *Pipunculidæ* and *Diopsidæ*.

We have thus given what indeed may be considered as only a very general sketch, but yet a complete and faithful representation of the knowledge which, up to this time, we have been able to obtain of the Diptera of the Amber-fauna.

The Diptera in amber I consider as representing a fragment of a district fauna of the amber-period, which however owes its peculiar character to special local conditions.

The manner in which amber now occurs will very well allow us to assume that perhaps the bits found in any one place, or that at least those found in different places, may have been derived from localities quite far removed from each other. The known occurrence of enclosures which appear to be analogous to recent species of very different climates, seems to favor such a supposition. The proof of its correctness by the discrimination of the species, enclosed in amber derived from different localities, has so far been impossible, since only in a very few cases have we been able positively to ascertain the locality where the insect-bearing specimens came from. We had therefore, in order to obtain the desired result, to adopt a different mode of investigation.

If the species *a* is found enclosed in the same piece with the species *b*, while *b* has been found to occur in another piece together with *c*, we may presume that they belong to the same district-fauna. I have therefore devoted especial attention to those pieces of amber which contained several species, and have endeavored,

from their examination, to form a catalogue of the species which, under the above supposition, might be considered as belonging to the same district-fauna. Some very beautiful pieces of amber, containing each from ten to twelve species of *Diptera* have greatly aided me in this investigation. But among most of the amber collectors the unfortunate fashion prevails of dividing the larger pieces, containing several specimens, into smaller fragments in order to show each one by itself and to make a more convenient arrangement in the museum. The loss to a true scientific investigation of the Amber-fauna by this mode of proceeding has been so great that I cannot use too strong language in protesting against it. Although the catalogue thus formed does not by any means embrace all the species, it is yet comprehensive enough to enable me fully to confirm the supposition that the *Diptera* which are found in Prussian amber belong to one and the same district-fauna.

The assumption that the Amber-diptera represent a fragment only of such a district-fauna, dependent upon special and yet uniform local conditions, must be considered as established, if the composition of this fauna evidently suggests coincident conclusions as to the nature of these local conditions; or, in other words, if it can be proved that the Dipterous fauna of the amber is composed of the different families, just in the same manner as families of recent *Diptera* would enter into the composition of a fauna, subject to certain local conditions.

Now, the composition of the Dipterous fauna of the amber is indeed precisely such, as forcibly to suggest some conclusions about the nature of the localities in which it flourished and in which the amber now enclosing it was formed. The great prevalence of the *Diptera nemocera*, both in the number of species, and still more of specimens, affords us in this respect an important indication. Most of these species are but poor flyers, never rising to a great height, preferring moist places, sheltered from the wind, and appearing in vast numbers only under such circumstances. The idea which the especial abundance of the *Diptera nemocera* has suggested, as to the nature of the locality in which they once lived, is fully confirmed in other ways. As at the present day, the more delicate species of *Empidæ*, *Hybotidæ*, and *Tachydromidæ*, seek with peculiar preference the hovering places of the *Diptera nemocera*, on the borders of ponds grown up with vegetation, or the shelter of the denser forests, so too they are found in abundance in amber. Of the *Dolichopodidæ*, those species are quite absent which live principally upon the water, or on water plants, while of those more active forms which swarm in open spots, there are only a few scattered representatives; on the contrary, of those genera whose species at the present day are found lurking for their prey in swarms on the

trunks of trees, sheltered from the wind, the number of species, and still more of individuals, is quite considerable. The abundance of those Diptera whose larvæ live in rotting wood, and the countless swarms of *Mycetophilidæ*, bear testimony of the dampness of the locality and of the predominance of fungus-vegetation. Other Diptera, whose larvæ live in standing or slowly flowing waters, show that such were not wanting, while the larvæ of some species, if the analogy with those now living does not fail, must have had their abode in more rapid currents.

If the presence of the Diptera just enumerated furnishes positive testimony as to the local conditions, so does the great rarity or total absence of other families of Diptera, afford a hardly less important negative testimony to the same effect. It is remarkable enough with what absolute distinctness all of those Diptera are wanting in amber which prefer open swarming places, exposed to the sun, or select arid spots. So of all the genera of *Anthracidæ*, there has been found but a single species, and that has been met with only twice. Of *Asilidæ*, of which only a few decidedly prefer to dwell in places such as have been just described, four species have been found. The very rare occurrence of the *Dexidæ*, the *Muscidæ*, and the *Tachinidæ*, as well as the limitation of the *Syrphidæ* to a very narrow series of forms allied to *Xylota*, appears also to depend upon the preference which the majority of the species belonging to these families, have for open, sunny localities, abounding in flowers. Their greater strength and power of flight may have rendered their escape possible, when species not so well provided would have certainly been enveloped, but this difference is not sufficient ground for their unfrequent occurrence in amber, if we assume that the species of these families were already abundant in the Amber epoch, while under the same supposition we could explain it by the controlling influence of special local conditions. The numerous and very varied forms of the *Cecidomyidæ*, whose species are strictly confined each to its peculiar plant, teach us that the flora was one rich in species; this decidedly removes the supposition of the exclusive presence of extensive coniferous forests and renders it certain that leaf-bearing phanerogamous plants, if not abundant in numbers, were at least rich in species, while it is by no means apparent that they all had the arborescent form. Next to the *Cecidomyidæ*, the species of no other family are so intimately connected with particular plants as those of the *Trypetidæ*, whose larvæ have an especial preference for the *Synantheræ* (*Compositæ*) as an abode. These are entirely wanting in amber. From this to pronounce upon the total want, or even the rarity, of *Synantheræ* in the Amber period, would be a too rash conclusion; moist and shady places are avoided by these insects, who seek the plants, which are to be the residence

of their progeny, in open and sunny spots, and hover about these plants, or at least in their neighborhood, with great pertinacity. Thus their absence from amber is only one more striking testimony to the above-mentioned conditions of the locality in which the Amber-diptera lived.

These minute beings of a long by-gone age, preserved to us in the form of mummies, afford us also some glances into the scenes of the animal life of that time. That the warfare between those of their own kind, still going on in our days, had even then begun, is shown by the swarms of *Leptidæ*, *Empidæ*, *Hybotidæ*, *Tachydromidæ* and *Dolichopodidæ*, which prey upon other Diptera. That this war was even then declared against other orders of insects, is seen from the presence of powerful *Asilidæ*; that there was a war waged against them, in which too they were not victors, is learned from the number of spiders found with them. An insect of the genus *Silvius* (*Tabanidæ*), whose female certainly could not have failed to quench her thirst for blood, shows that some of the larger mammals must have lived there, while the complete absence of the genera *Stomoxys*, *Scatophaga* and *Borborus*, as well as of all the *Æstridæ*, does not render it probable that they were in very great numbers.

We behold then the Diptera, now entombed in amber, in their once living swarms, in strife among themselves, at war with others, sometimes conquerors, sometimes vanquished, in a damp region, where fungi grow abundantly, sheltered from the wind by thick forests, surrounded by a phanerogamous flora, rich in species; and we involuntarily ask, In what sort of a climate lay this paradise for long-legged gallinippers and impudent gnats?

If we had any reason to consider the now extant amber-diptera as representatives of a district fauna in general, instead of taking them merely for specimens of a fragment of such a fauna, a fragment dependent on, and limited by local influences, our conclusions about the climate of that district would be essentially different. The prevalence of the *Diptera nemocera*, as to the number of species as well as individuals, the great rarity of *Asilidæ*, and still more of the *Bombylidæ*, the absence of all *Nemestrinidæ*, etc., would undoubtedly have indicated a climate somewhat colder than the present climate of Prussia; the appearance of some forms, reminding of warmer climates, would in such a case have been but of little importance, as even now the higher latitudes harbor some forms of this kind. I believe I have proved sufficiently that the local influences which limited the composition of the amber-fauna, have to be taken into account in drawing our conclusions. Then, the prevalence of the *Diptera nemocera* will lose the importance which it otherwise would have had; for also in present times, localities of the above indicated description, even in much lower latitudes, show this

prevalence in the same degree; at the same time, the presence of a number of Diptera, closely related to some southern species, will gain so much the greater importance, since the rarity of their occurrence in amber merely proves their rarity in the specified local conditions, without excluding the possibility of their common occurrence in other localities as well as of the occurrence of many other species not preserved in amber. The following species may be named as indicative that the climate of the Amber period was very probably somewhat, although not very much, warmer than the present climate of Prussia: 1. *Styrimomyia gracilis* and the species of *Diplonema*, the close relatives of which occur in copal. 2. Species of *Plecia*, closely allied to those occurring in warmer latitudes. 3. *Sphyracephala*, a close relative of *Sphyracephala brevicornis*, Say, common in the middle and southern of the United States, the only living representative of the genus as yet known. 4. A species of *Corsomyza*, the living representatives of which belong to the Cape of Good Hope; they show, however, considerable structural differences from *Corsomyza crassirostris*, enclosed in amber. 5. Several *Cyrtidæ*, of the section *Cyrtina*, more numerous represented now in countries the temperature of which is at least equal to that of the southern peninsulæ of Europe.

An especial interest is afforded by the comparison of the Amber-diptera with the fossil Diptera of the tertiary period, found in other localities. I have been able as yet to subject to a close and careful scrutiny only the fossil Diptera found near Radoboj in Croatia. The collection of these Diptera belonging to the Imperial Mineralogical Institution in Vienna contains the types of the species determined and described by Professor O. Heer. The result of my researches is, that the Diptera of Radoboj afford only a very indistinct insight into a still more localized fauna; that there is not a single genus among them which does not likewise occur in amber; that although some species from Radoboj are pretty nearly allied to species enclosed in amber, the identity of such species cannot be proved at present, and probably never will be proved, on account of the difficulty of comparing specimens in so very different conditions of preservation. Of the more striking forms found in amber, those especially which do not belong to the European fauna, as far as known at present, none had been discovered in Radoboj, with the single exception of some species of *Plecia*.

I will proceed now to the comparison of the Amber-diptera with those of the present age. If it were possible to compare the complete fauna of the Amber period with the now living Dipterous fauna of the globe, and, by such a comparison, to find out which of the families and genera have died out, or at least have become scarcer in the number of species, and in which the

number of species has increased, or even what new forms have been added to the previously existing ones, such a comparison would of course afford the highest interest. But, unfortunately, such an attempt is impossible, on the one side because of the as yet very imperfect knowledge of the now living *Diptera*, on the other, because what we know of the Amber-*Diptera* is but a fragment of a district fauna. In confronting, therefore, both faunas, I will by no means try to discover and to establish differences between them of the above indicated kind, which would be a useless attempt; my only aim will be to refute as erroneous certain conclusions as to the existence of such differences. Among such conclusions I will especially advert to the two following: *first*, that in the Amber period the relative proportion of the *Diptera nemocera* to the *Diptera brachycera* was greater than now; *second*, that during the Amber period the limit between the two sections of the *Diptera* was less definite, more obscured by intermediate forms, and that it became better defined only at a later epoch, through the disappearance of those intermediate forms.

The reasons why I do not adopt the former of these conclusions result from my foregoing deductions, and it is unnecessary to dwell upon them any longer. But I have to make some remarks about the other conclusion, inasmuch as formerly I was myself not disinclined to favor it, although I reject it now as founded upon erroneous premises. For a long time students of systematic Dipterology were wont to look upon the boundary line between those two sections, with regard to the living fauna, as a very well defined one, excluding any intermediate forms. My first researches among the Amber-diptera brought about the surprising discovery of two species, showing a distinct transition between the two sections. I founded two new genera upon them, one of which I called *Electra*, in allusion to the Greek word for amber, and the other *Chrysothemis*, to indicate its close relationship to *Electra*. Both combine the many-jointed antennæ of the *Diptera nemocera* with the general structure of the *brachycera*. As long as no similar forms among the living *Diptera* from all parts of the world had been discovered, there was indeed some reason to suppose that the limit between the two sections was sharper now than in the Tertiary period, although our very incomplete knowledge of the living Dipterous fauna required some caution in drawing this conclusion. This caution was justified subsequently by the discovery of a North American species, published by Mr. Haliday under the name of *Rachicerus fulvicollis*, a species which not only forms a most decided transition between the two principal sections of *Diptera*, but shows even the closest relationship with *Electra* and *Chrysothemis*. My own studies of the North American fauna have

made me acquainted with three other intermediate forms of this kind, two from the United States and one from Cuba. These species also belong to the relationship of *Electra*, *Chrysothemis* and *Rachicerus*, although they cannot be referred to either of these genera, so long as their present distinction, based upon the structure of the antennæ, is maintained. The great diversity which they show in the structure of that organ, by the conformation of which they are distinguished from the whole tribe of the *Diptera brachycera*, is striking, but not without analogies. The sections of the *Diptera nemocera* and *brachycera* are therefore connected by intermediate forms in our times, just as they were so in the Amber period, only these intermediate forms being foreign to the European fauna, were discovered in amber first, and afterward among the living insects.

That among the amber Diptera there are many genera of which no living representatives are as yet known is beyond question; I have had occasion to state this fact more in detail in my "Observations on the Dipterous fauna of the Amber," published in 1850. A part only of these genera owe their existence to the necessity of establishing for these fossil species generic distinctions based upon slighter plastic characters than those usually admitted for the separation of living species, and have therefore less claim to be taken into consideration here. Another portion consists for the most part of very striking species, easily distinguished from all the known living genera. But this circumstance does not justify the conclusion that such Diptera are really strangers to the living fauna of our age; on the contrary, the results already obtained by the heretofore very incomplete investigations, authorize the supposition that these genera may yet be found among living species. Several of these interesting genera have already their little history. May I be allowed to mention here some facts of this kind.

One of the most curious discoveries made in amber is a remarkable genus, situated near *Cænomyia* and for which I have proposed the name of *Arthropeas*, on account of its peculiar subuliform antennæ. After having found *Arthropeas nana* in amber, I received a closely allied species from Eastern Siberia, *A. Sibirica m.*, and now I possess in *A. Americana m.*, a species from the United States which is even somewhat more nearly related to *A. nana*.

The genus *Bulbomyia*, two species of which occur in amber, was remarkable for the difficulty of assigning a suitable location for it in the system, as among all the living Diptera no closely allied genus could be found. Of this genus I likewise possess now a North American species, unfortunately in a single specimen, the state of preservation of which does not allow a close comparison.

Diplonema, remarkable for the elegant structure of its antennæ, is one of the most striking genera of *Psychodidæ* found in amber; *Styringomyia*, a genus of the *Tipulidæ*, has a very peculiar neuration of the wings; both genera when I discovered them in amber were new. I was not a little surprised therefore when I found specimens of both genera together, enclosed in a lump of copal. Unfortunately it was not possible for me to ascertain the country where this piece of so-called East Indian copal came from, although I still hope that a well-preserved beetle, contained in it, may help to solve this question.

Among the amber Diptera I also found three species of a Tipulideous genus, which I called *Toxorhina*; it is remarkable for its long, almost filiform, stiff proboscis, for the peculiar structure of its oral organs, and for the abnormal neuration of its wings. Later, I became acquainted with a living representative of this genus in *Toxorhina fragilis* from Jamaica, and still later I was led to recognize that Westwood's genus *Limnobiaorhynchus*, founded upon a Canadian and a Brazilian species, was, if not identical, at least very closely related with *Toxorhina*.

Another very remarkable genus among the number of the *Tipulidæ* occurring in amber, is the new genus *Macrochile*. A closely allied genus was recently described by Baron Osten Sacken, in the Proceedings of the Academy of Natural Sciences of Philadelphia, under the name of *Protoplasa*.

These instances, which could be increased by many others, will be sufficient to prove that it would be premature to conclude from the presence in amber of a number of genera, the living representatives of which have not yet been found, to the non-existence of these genera in the fauna of the present epoch.

The result therefore to be drawn from the foregoing facts and from the considerations connected with them, is in general of a rather negative nature; and this result is, that the facts in our possession do not justify any conclusion as to the existence in the Amber period of forms totally different from those now living in any important parts of their organization—or, to adopt a more positive mode of expression, it seems extremely probable that the generic types which existed in the Amber period, have been preserved down to our time. The question whether the number of generic types has been perceptibly increased since the Amber period cannot be discussed at all, as we possess but a small fraction of the fauna of that time.

If the generic types of the Diptera of the Amber period have thus been preserved to our time, the question naturally arises whether this is not also the case with the specific types, if not all, at least some of them. The general impression produced by the amber Diptera, even in a cursory examination, has so little of the character of novelty in it that we at once feel disposed to

raise this question and to proceed to the comparison with living species. Since the very beginning of my researches, that is, about seventeen years ago, I have very closely pursued this comparison. I early found that some of the species enclosed in amber are not only closely allied to living species, but that they are surprisingly like them, and several such species, (*Mochlonyx atavus* with *M. velutinus*, *Diplonema longicornis* with *D. eucerus*, *Styringomyia gracilis* with *St. pulchella*,) were already at that time noticed by me. Their number has since considerably increased. At the same time however, with the acquisition of better specimens, or of such as allowed a closer scrutiny of parts important for the discrimination of species, it became apparent that slight differences could always be discovered, preventing the assumption of the specific identity of amber Diptera with the living species most closely resembling them.

Those acquainted with the extreme difficulty attending, in many cases, the discovery of definite plastic characters for the discrimination of undoubtedly different species of living Diptera, will justify me if I attach less importance to the result of a single comparison of a fossil species, contained in amber, with an extremely resembling living one, than to the general average of the results of such comparisons. And this is, as already noticed above, that with the increase in quantity as well as in quality of materials for comparison, the differences which could be traced became gradually more definite than they were before, with poorer materials. Thus, not only do we not possess any sufficient proof of the identity of any one species, contained in amber, with a living one, but the results heretofore obtained render it extremely probable that a still greater increase of materials for investigation will enable us to discover specific distinctions even in the few cases which appear as yet doubtful.

Nevertheless the relation between the amber Diptera and the living species so closely resembling them is a very peculiar one. It consists for the most part chiefly in a somewhat different shape or a different relative size of one or several parts of the body, the structure of the whole and the shape of the other parts being most remarkably similar. The relationship, therefore, between such species is so strikingly close, that it naturally suggests the idea of a genetic connection, and maintains it against all possible theoretical objections. The impression that the living species, connected by such a close link of relationship to some amber Diptera, are not new additions to the number of old species, but are so to say, the transformed old species, is in my opinion irresistible to any unprejudiced observer.

The researches on the geographical distribution of the living species so closely related to some species enclosed in amber, lead to a very remarkable result. The gradual development of this

result in the course of my researches took place as follows. It appeared at first that the living species of the indicated kind were scattered irregularly and at random over all the parts of the globe. Further inquiry not only increased the number of such related couples of species, but allowed also very frequently to replace the living species of some previously discovered pair by some other, still more closely allied to the fossil one. The further the research was pursued in this direction, the more it became evident that the living species of these pairs have a very definite geographical distribution, as being gradually eliminated from the other parts of the world, they tended more and more to concentrate in Europe, and in a much higher degree in North America.

I readily acknowledge that my researches have necessarily been influenced by a purely personal coefficient, which has to be taken into account, in order to establish the absolute value of the result obtained. This personal coefficient consists in the numeric proportion of the living species from different parts of the world, which could be subjected to comparison, as well as in the more or less complete knowledge I had of the Dipterous faunæ of the different continents. The European Dipterous fauna is naturally the best known to me; next comes the North American fauna, which I know better than that of all other extra-European countries, excepting perhaps that of the Cape, as I possess from that region more than 800 species, collected within a comparatively limited territory. It is therefore unquestionable that the result obtained by me requires a correction, before it can have a claim to an absolute value. But should I even introduce this correction in the highest measure admissible, still enough will be left to enable me to assert with the utmost certainty that those among the living *Diptera* which most closely resemble the amber *Diptera*, abound in a most prevailing degree in North America and especially between the latitudes of about 32° to 40°; that a more limited number belong to Europe, and that, among the *Diptera* of the other parts of the world, heretofore none can be pointed out which stand to amber *Diptera* in the same relation of extremely close resemblance, as some European and North American species, and only very few to which some amber *Diptera* are more allied than to any other known living species.

The facts just explained become especially striking through the circumstance that those genera of amber *Diptera*, which do not occur in Europe, and which for this reason attracted more attention from European students, were in part discovered in America, and are in part replaced there by closely allied genera. With regard to this, I will remind only of what has been said above on the genera *Diplonema*, *Toxorhina*, *Styringomyia*, *Elec-*

tra, *Chrysothemis*, *Arturopeas*, *Bolbomyia* and *Sphyracephala*. The contrast between the close relationship of the North American Diptera with those of the amber on one side, and on the other the almost absolute absence of any such connection between the amber fauna and the living Dipterous fauna of the other parts of the world, this contrast is strikingly illustrated by the fact that among more than 800 species from the Cape closely scrutinized by me, there was not a single one which showed any remarkable degree of proximity to species contained in amber. The species of *Corsomyza*, at home in that region, are without exception the only ones which are represented by a Dipterous in amber, more allied to them than to any other kind at present known. We may therefore safely adopt as a final result of the researches made by us, and one that will probably be never controverted, that the amber Diptera stand in a much closer relation to the North American and to the European Diptera, than to those of any other fauna. This relation proves to be, in Europe as well as in North America, identical in its nature, and to any observer, unprejudiced by theories, irresistibly suggestive of a causal connection; it only differs in degree—the relation with the North American fauna being so much richer in points of contact, and therefore so much closer, than that with the European fauna.

This peculiar double relationship of the amber Diptera with the Diptera of North America and of Europe, two parts of the world separated by an ocean, led me to a closer comparison between the faunas of these continents, the results of which comparison I intend to submit in a detailed report on some other occasion. However, as these results have some connection with my researches on the amber Diptera and contribute to complete the sketch of the relation between the latter and the living species, I may be permitted to encroach a little longer upon the patience of my hearers, and to explain to them, omitting all detail, the progress of this new research and the principal facts elicited by it.

The comparison of the North American Diptera with the European ones was rendered possible to me, on a very extended scale, through the study of the collections of Baron Osten Sacken; this comparison showed a surprisingly large number of species common to both continents.² Besides these species,

² As such species, common to both continents, I can name with certainty and from personal investigation, the following: *Anopheles maculipennis* Meig., *Anopheles quadrimaculatus* Say (= *pictus* Lw.), *Anopheles nigripes* Staeg., *Tanytus choreus* Meig., *Ceratopogon lineatus* Meig., *Cecidomyia destructor* Say (= *funesta* Metch., = *secalina* Lw.), *Scatopse atrata* Say (= *recurva* Lw.), *Scatopse notata* Linn., *Aspites borealis* Lw., *Rhyphus fenestralis* Scop., *Rhyphus punctatus* Meig. (= *marginatus* Say), *Cenomyia ferruginea* Fab. (= *pallida* Say), *Sargus viridis* Say (= *frontalis* Lw.), provided the specimen, communicated to me as European, really belonged to the old world, *Eristalis ceneus* Scop. (= *vincerus* Harris), *Imatisma pos-ticata* Fab. (= *cimbiciformis* Fall.), *Syrirta pipiens* Linn., *Xylota pigra* Fab. (= *hæ-*

absolutely identical and showing no difference whatever, a large number of species has to be recorded, which, if they had been found in Europe, would certainly have been considered only as slight varieties of other well-known European species, as their only deviation merely consists in a slight difference of coloring; but this difference being a very constant one, it becomes extremely difficult to decide whether such species should be considered as specifically distinct from the corresponding European species, or as identical with them.³ A third, not less numerous category of species, shows, besides these slight but constant differences in coloring, some very insignificant plastic discrepancies; for instance, in the size, in the length of the hairs on the body, in the relative length of the wings or the legs to the whole body, etc., differences which, in order to be brought to light, sometimes require the comparison of a whole series of specimens.⁴ A fourth

matodes Fab.), *Platychirus granditarsus* Först., *Brachyopa ferruginea* Fall., *Scenopinus fenestralis* Linn. (= *pallipes* Say), *Scenopinus laevifrons* Meig., *Dolichopus brevipennis* Meig., *Dol. plumipes* Scop., *Dol. discifer* Stann., *Scellus spinimanus* Zett., *Psilopus pallens* Wied., (= *albonotatus* Læw), *Oestrus bovis* Fab., *Cephalomyia Ovis* Linn., *Gastrophilus Equi* Linn., *Melanophora roralis* Linn., *Pollenia rudis* Fab., *Musca domestica* Linn., *Cyrtoneura mediatubunda* Fab., *C. stabulans* Fall., *Mesembrina resplendens*, *Stomoxys calcitrans* Linn., *Anthomyia diaphana* Wied., *Anthom. stygia* Meig., *Aricia morioides* Zett., *Hylemyia Angelica* Scop., *Hydrotæa dentipes*, *Hylemyia urbana* Meig., *Homalomyia canicularis* Lin., *H. subpellucens* Zett., *H. manicata*, *H. scalaris* Fab., *Hydrotæa armipes* Fall., *Ophyra leucostoma* Wied., *Lispe uliginosa* Fall., *Scatophaga squalida* (= *S. furcata* Say ?) *Scatophaga stercorea* Lin., *Cordylura hircus*, *Sapromyza lupulina* Fab., *Scyphella flava* Linn., *Lauzania cylindricornis* Fab., *Lauzania frontalis* Lw., *Psila bicolor*, *Sciomyza nana* Fall., *Sciomyza obtusa* Fall., *Sciomyza albocostata* Fall., *Dryomyza anilis* Fall., *Blepharoptera iners*, *Ortalis vibrans* Linn., *Ortalis cana* Lw., *Piophilæ Casei* Linn., *Piophilæ nigriceps* Meig., *Piophilæ petasionis* R. Desv., *Heteroneura albimana*, *Borborus equinus* Fall., *Drosophila ampelophila* Lw., *Dros. transversa*, *Dros. graminum*, *Stegana nigra* Meig., *Stegana hypoleuca* Meig., *Dichata caudata* Fall., *Dichata brevicirca* Lw., *Scatella quadrata* Fall., *Scatella Stenhammari* Zett., *Ochthera mantis* Deg., *Ilythea spilota* Hal., *Melophagus ovinus* Linn., *Olfersia Ardeæ* Macq., *Hippoboscæ equina* Linn.

Besides a great many other species, the occurrence of which on both continents is recorded with less certainty, the following European species are found in Greenland, according to Stæger's trustworthy statements:—*Diamesa Walilii* Meig., *Chironomus byssinus* Meig., *Chironomus aterrinus* Meig., *Chironomus picipes* Meig., *Trichocera maculipennis* Meig., *Sciara flavipes* Meig., *Calliphora erythrocephala* Meig., and *Phytomyza obscurella* Fall.

[*Rhipidia maculata* M. and *Symplecta punctipennis* may be also added with certainty.—O. SACKEN.]

³ As instances of such species may be recorded here: the North American *Subula pallipes* Læw, and the European *S. marginata* Meig., *Chrysotoxum* sp. indescr. and *Chrysotoxum bicinctum* Linn., *Tetanocera pictipes* Læw, and *T. Umbrarum* Linn., *Tetanocera saratogensis* Fitch and *T. Pratorum*, Fall., *Hemerodromia valida* Lw. and *H. Frigeli* Zett.

⁴ Here may be named: *Bombylius fraterculus* Wied. and the European *B. major* Linn.; *Chrysotoxum* sp. indescr. and *Chrysotoxum fasciolatum* Deg., *Helophilus* sp. indescr. and *H. frutetorum* Fab., *Lucilia* sp. indescr. and *L. cesarion* M., *Cyrtoneura* sp. indescr. and *C. assimilis* Fall., *Gymnosoma par* Walk. and *G. rotundata* Linn., *Cordylura* sp. indescr. and *C. pudica* Meig., *Allophyla laevis* Lw. and *A. nigricornis* Meig., *Trypeta fratria* Lw. and *T. Heraclei* Linn., *Ortalis rufipes* Læw and *O. marmorea* Fab., *Drosophila* sp. indescr. and *D. funebris*, *Ephydra atrovirens* Læw and *E. micans* Hal. and many other species.

group may be formed of the likewise very numerous species which, although so like some European species as to be at first glance mistaken for them, show upon nearer examination very definite plastic characters. The discovery of these characters often requires a great deal of attention; nevertheless they are of such a nature that the comparison of even single specimens leaves no doubt as to their specific differences.*

The large number of species contained in all the four groups shows that the Dipterous fauna of North America is not only very much like the European fauna, but that there is between them a relationship of a more intimate kind, which is to be compared only with that uninterrupted succession offered by the Dipterous fauna of the whole northern part of the Old World. There are no other two countries on the whole globe, so far removed from each other and showing at the same time anything approaching this relationship in the Dipterous faunas; generally other countries have but a small number of such species in common, which occur in both in absolutely identical specimens or only slightly different in coloring; otherwise their faunas have no points of contact whatever.

In order to form a more definite opinion on the origin and the nature of this close connection between the Dipterous faunas of Europe and America, it is necessary to elucidate somewhat more in detail the facts relating to this connection.

The laws regulating the distribution of the Diptera are somewhat different from those of the other orders of insects; and this difference is due to the considerable power of flight which many Diptera possess, and to the simplicity of the conditions under which they can live and their brood can prosper. As the *Libellulidæ* show in this respect the nearest approach to them, the laws of their geographical distribution may also be the nearest to those of the Diptera. The latter laws differ from those of the other orders of insects, by the wide area of distribution of the single species and by the configuration of these areas. They are not nearly the same for the species of all families, but vary according to families, so that the *climatic character* is most clearly expressed in those which have the smallest area, as for instance in the family of *Asilidæ* and some others. Although it can be admitted, as a general rule, that the extent of the area of distribution is in direct proportion to the power of flight and the sim-

* As instances of such species may be named: *Chrysopila quadrata* Say and *Chrysopila nubecula* Fall. *Leptis vertebrata* Say, and *Leptis annulata* Deg., *Leptis scapularis* Lœw and *Leptis lineola* Fab., *Atherix vidua* Walk. and *Atherix immaculata* Fab., *Arthropeas americana* Lœw and *Arthropeas sibirica* Lœw, *Chrysotoxum pubescens* Lœw and *Chrysotoxum octomaculatum* Curt., *Volucella evecta* Walk. and *Volucella bombylans* Linn., *Helomyza assimilis* Lœw and *Helomyza Nemorum* Meig., *Helomyza lateritia* Lœw and *Helomyza flava* Meig., *Sepedon pusillus* Lœw. and *Sepedon spinipes* Scop., *Philygria opposita* Lœw and *Philygria punctato-nervosa* Fall.

plicity of the conditions required for the existence of a species, still some families show in this respect peculiarities which do not find a satisfactory explanation in those two causes.

On account of the very great extent of the area of distribution of the Diptera in general, the faunæ of distant countries have many more species of this order in common, than of any other order of insects. The same causes on which this extent of distribution depends facilitate even in our days the importation of Diptera much more than that of other insects, through the intercourse between countries. It is well known that *Musca domestica* has followed the European settler everywhere. Wherever man penetrating into distant countries has carried provisions of smoked meat and cheese along with him, *Piophilæ Petaionis* and *Cusei* have accompanied him. They occur in Greenland, as well as on the Galapagos Islands, in the land of the Egyptian Fellahs as much as in the backwoods of North America. Where horse and sheep have become acclimated, *Gastrus Equi* and *Cephalomyia Ovis* have settled with them. *Bombylius punctatus* and *Toxophora maculata*, the powers of flight of which acquire, with the increase of heat, very great energy, are found everywhere between Southern Europe and the Cape, and the beautiful *Symmetus costatus* is found together with them, from Spain to the southern extremity of Africa. The barrier of a sea is not sufficient to stop the progress of the unwieldy *Olfersia Ardeæ*, as it has the heron for conveyance, and *Anaplera pallida*, although unable to fly, occurs wherever the swallow builds its nest. The simple conditions required for the existence and the reproduction of *Medeterus inæqualipes*, common on the shores of Sweden, allowed this species to spread all over the coasts of Europe and of Africa, as far as the Whale Bay. The species living on cultivated plants have acquired a wide area with them, as for instance several of *Oscinis* and *Chlorops* with the cereals, also the noxious *Cecidomyia destructor*. *Petalophora capitata* occurs wherever the orange and the lemon are cultivated and with the extension of the culture of the olive-tree, *Dacus Oleæ* has followed it.

It would be easy to multiply instances of this kind. Those above given are however sufficient to show that immense distances and wide seas are no insuperable obstacles for the spreading of Diptera, and that a lively shipping intercourse between two countries may easily carry over species from one fauna into another, and, the circumstances being favorable, even permanently colonize them. It is no wonder therefore that America, which for a considerable period of time has been in constant and always increasing intercourse with Europe, should have with the latter so many species in common. It would be more wonderful if this had not taken place. But a different question is,

whether the existing intercourse between the two continents is sufficient to account for the large number of species common to both. I am satisfied that it has to be answered negatively.

In order to investigate the influence of a prolonged intercourse of this kind between two countries separated by a sea, I have repeatedly directed my attention to the comparison of the Dipterous faunas in the countries surrounding the Mediterranean. These investigations, for which I possess abundant materials, have made me, as far as it was possible, thoroughly acquainted with the influence exercised by an intercourse of this kind on the intermingling of the faunas, and have afforded me a measure of this influence. In drawing a conclusion from the extent of these influences in the countries adjacent to the Mediterranean, to the extent of the same influences as existing in consequence of the intercourse between Europe and America, we have to take into account the comparatively recent epoch when this latter intercourse began, the much greater distance between the two continents, and before all, the much greater length of time required for a passage between them, especially in former years. In view of all these causes, tending to diminish the probable influence of the intercourse on the intermingling of the faunas, we cannot possibly admit that the occurrence of such a large number of species, common to both sides of the ocean, should be merely the result of an intermingling brought about by this intercourse. It should be borne in mind that it is not with one or two dozens of species that we have to deal, but with a number already reaching the second hundred, and that such species, found on both continents, far from being, in either of them, rare guests of sporadic occurrence, are equally common in both, so as to necessitate a serious revision of the synonymy of the described European and North American species. I will readily admit that *Musca domestica*, *Cyrtoneura Hortorum*, *C. meditabunda* and *C. stabulans*, as well as *Pollenia rudis*, have been imported from Europe to America; it can hardly be doubted that *Scenopinus fenestralis* and *S. lævifrons* can easily be brought over in ships; the conformity of many species of *Scatophaga* and of *Barborus* can be explained in the same way; the reason of the occurrence of a number of the same species of *Drosophila*, in both countries, is easily found in their mode of life; nor will it appear very extraordinary that *Drosophila ampelophila*, discovered by me in immense numbers in the raisin-stores of Smyrna, should be a common insect in Cuba; it is also a fact, that the North American *Mallota posticata* has been several times caught in Europe and described as a European species, under the name of *M. cimbiciformis*; that *Eristalis æneus*, not rare in North America, should be a descendant of European parents, is easily possible, as a ship affords the necessary conditions for the preservation of the larvae. It

will be more difficult, however, to explain how *Ilythea spilota*, *Dichæta caudata* and *D. brevicauda*, *Ochthera Mantis*, etc., should have crossed the sea. The importation of some species, as, for instance, of the beautiful *Psilopus albinotatus*, discovered by me in Rhodus, seems almost inexplicable, and still this species is perfectly identical with the North American *P. pallens*. That all the species, now occurring on both continents, should have been gradually carried over from one to the other is utterly improbable. If we admitted this supposition, then, considering the large increase of the intercourse within more recent time, and the shortness of the passages now attained, we should also admit that most cases of importation have taken place, if not within the last ten or twenty years, at least during the last half a century, and secondly, we would have to infer that this importation of species was a reciprocal one. But if the latter was the case, the study of the European Diptera would have long ago detected the existence of these large importations from America; the Dipterous fauna of England especially, owing to the most frequent intercourse of this country with America, would have shown evident traces of such exchanges of species; in our sea-ports likewise, the appearance of single species of recent importation would have been noticed and their spreading from these centres, observed. Although I readily admit that the knowledge of the European Diptera is still very imperfect, nevertheless occurrences of this kind, owing to the large number of cases, would not have escaped attention. We have to conclude then, for the present, that the importation of species through the agency of frequent intercourse, does not afford a sufficient explanation of the large number of species common to Europe and North America.

As to those North American species, which are distinguished from European ones merely by a difference in the coloring, the question arises, whether they can be considered as descending from the same stock. It is an undoubted fact that species with a wide area of distribution show, in very remote parts of this area, a perceptible difference in coloring, sometimes even a very decided aberration in the picture. Such is, for instance, the case with *Anthrax bifasciata*, which shows toward the east a much more pronounced contrast between the white and the black coloring of the body, and acquires besides some slight, but very definite, peculiarities in the picture of the wings, so that an eastern specimen can be immediately recognized among a number of German ones.—Still better known is the influence which certain regions exercise on the coloring of all the species occurring there; this is, for instance, in a very striking degree, the case with Iceland. A collection from that country, at a cursory view, seems to contain many new species, but upon closer examination, these spe-

cies prove to be merely varieties of well known European species; they owe their existence to the propensity of all colors to merge into black and to the greater extent and intensity of the black itself, so that a light-colored picture upon black ground becomes much narrower or even disappears altogether. It can be likewise shown, that more confined localities exercise a similar, although less pronounced, influence on the coloring of the species. Under these circumstances, the question whether the North American species, above alluded to, are of the same descent with the corresponding European species, must be answered by an affirmation.

The same question may be proposed about those North American species which deviate from European species only by slight plastic differences, often merely a small variation in the size of some organ, or in the length and density of the hairs and bristles. Similar modifications are sometimes observed among specimens of European species. Thus the specimens of *Gymnopternus Sahlbergii*, caught in the southern parts of Switzerland differ so much from the Swedish specimens by the hairs and bristles on the first joint of the middle tarsi of the male, that they might be taken for different species, if all the intermediate forms did not occur in the countries lying between those two extremes. Still more striking is the difference between the male specimens of *Empis maculata* Fab., (not the *Empis variegata* confounded with it by Meigen,) caught in southern Germany and Sicilian specimens, the latter having on the fore tarsi hairs of unusual length and stoutness; the specimens from Lombardy are still a good deal like those from southern Germany; in those from Florence the hairs on the fore tarsi are already quite conspicuous, and they are still longer in the specimens from Rome, so that in this case the specific identity is proved by a gradual transition. Under such circumstances, the question, whether species showing but slight differences of the indicated kind should be considered as derived from the same stock, cannot be answered negatively. I readily acknowledge that it is rather difficult to state modifications of what parts in the Diptera have to be considered as essential and which as unessential, as different rules prevail in this respect in every family, in many families even in every genus, rules which a special research alone can determine. The only tolerably reliable general law prevailing in this case is, that all modifications in the structure of the mouth or of the genital organs are of the highest importance, whilst, on the contrary, all the other differences, observable even in the two sexes of the same species, are the least important.

We have now reached the category of those North American species which show a great resemblance to European species, but possess at the same time very definite plastic distinctive

characters; for brevity's sake I will call them *analogous* species. If we put now the question, whether it is to be assumed, that such analogous species may possibly have a genetic connection, we will find that all observations hitherto made on living Diptera warrant a negative answer. There is not a single instance on record which would justify the conclusion that under the now prevailing natural conditions, any species could be modified in that way, either through climatic influences, or in consequence of a compulsory change of food or through the contact with some other species. I do not deny that every time I compare such analogous species, the question forces itself upon my mind whether that, which seems impossible now, was not possible at some former period, as the impression left by such a comparison is most decidedly that of a common origin.

The European and the American Dipterous faunæ always appear to me like two branches of the same stock, each having had a development of its own, very similar however to the development of the other. But if there really was such a common stock for both, it is to be sought among the Diptera of a former geological period, and if the European and the North American Dipterous faunæ are to be considered as branches of this stock, the necessary inference would be that at a former period Europe and America had a continental connection.

Are the amber Diptera preserved fragments of this common stock?—Did a continental connection between Europe and America really exist at the time when they lived?—Did the submersion of an Atlantis tear asunder the branches of this stock? Was this catastrophe accompanied by changes which modified the general laws of development of the common stock in such a manner as to produce a difference between the further development of the stronger American branch and of the weaker European one, a difference not excluding at the same time a great deal of analogy?

Allow me to conclude my discourse with these unanswered questions. All those problems to which the study of the living and fossil Diptera affords a solution, or at least seems to afford one, I have done my best to answer. In doing this, I purposely remained within the exclusive limits of Dipterology, partly owing to my conviction that the interest of truth is best promoted when one confines himself to the investigation and discussion of a question from the point of view of his own speciality, partly because condemned as I am to a total literary isolation and absorbed now for years with utterly unscientific occupations, I am but very imperfectly acquainted with the researches made in a similar direction, especially with those of later years.