Reflections on the Baltic Amber Inclusions.

By
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During the planning of the scientific study and description of the material of amber inclusions which has in recent years been established at the Zoological Museum, Copenhagen, the preparation of a card-index of the literature—not only that on the amber fossils, but the literature on all fossil terrestrial arthropods from the Tertiary and the Quaternary periods—proved desirable.

Various problems arose during the study of this literature. In the first place, the literature most frequently cited includes several papers which only quite briefly mention the fossils found without referring them to certain species, or the specific names mentioned are real n o m i n a n u d a. This is generally the case in the older literature, more especially in that dealing exclusively with amber, which evidently to a greater extent than usual is written by authors who regarded the biological aspect as less essential. This literature is of no value as an aid in our study of the biological evolution.

The authors who accompany their namegiving by more or less detailed descriptions and figures, are in the main referable to two categories: those whose working field comprises all, or at any rate very large groups of terrestrial arthropodes, and specialists who only deal with fossils referable to a minor systematic group, in many cases only a single insect family. The former category is chiefly met with in the older literature, but right up to the most recent time have papers of this kind been published; works published by specialists, however, constitute an increasing part of the total number of publications.

The specialist who has become trained through his studies of the systematics of the recent fauna, generally has a considerable knowledge of the morphology of his small group, and knows what aspects of the often highly defective fossils should especially be

studied; thus, he may utilise traces which non-specialists would hardly notice, and he may with authority declare a fossil to be of no value as an object of systematic study. This last-mentioned fact is not of the least importance, for in this way he may spare his science of the burden of superfluous descriptions and superfluous names. In addition, the specialist has the advantage that he is more capable than anyone else to view the fossils in relation to the recent fauna.

The advantage which the more comprehensive researcher has over the specialist is in the first place that owing to his knowledge and initiative a collective treatment of a newly collected material may be carried out in a comparatively short time, so that parts of it are not to wait for years till a specialist happens to take an interest in it. This is undoubtedly a very great advantage; but it is often dearly bought. For it is hard to believe that a research worker should master the whole insect system with the same authority as that with which the specialist masters his small group. I.a. the range of variation of the same morphological character may differ from one family to another, e.g. the degree of constancy of the wing ribs. A consequence of this is too often uncertainty in the descriptions and in the valuation of the available facts. An idea of the seriousness of this source of error is obtained when parts of such a comprehensive material is later revised by a specialist, e.g. the revision by Mayr of the Formicidae in the Radoboj material of Heer from the Croatian Miocene.

Thus, many monographic works highly increase the difficulties of the worker who tries to get a general idea of the significance of the fossils; they do not always furnish a reliable material, but give rise to obscurity, as we do not fully confide in them. Moreover, in a Europe repeatedly devastated by war important collections of valuable scientific material which once formed the basis of works of this kind, have been lost, and a needed revision is accordingly beyond the bounds of possibility. In my opinion this way of publication should belong to the past.

The hitherto oldest find of recent terrestrial arthropods is the cicindelid *Tetracha carolina* L. from Baltic amber; the specimen was determined by the specialist Walter Horn, and the correctness of his identification can hardly be disputed. The recognition of this highly prominent species renders it probable that less con-

spicuous species of our present-day fauna are concealed under synonyms, not only in the literature on amber insects, but also, and possibly in an even larger number, in the lists of other known fossil faunas from the Oligocene and the Miocene periods. It emphasises how significant it is that the scientist describing a fossil insect group is fully familiar with its recent representatives. The fact that to-day *Tetracha carolina* occurs exclusively in south-eastern North America, also shows that a quite different distribution of the fauna in the past than at the present day must be assumed; no find ought to surprise us.

An estimate of the percentage of recent species which may be expected to be found in the various Tertiary faunas, may be obtained by comparing the paleogeographical and paleoclimatic conditions with the character of the recent fauna.

The phenomenon boreo-Alpine species is well known within many groups of terrestrial animals, not least within the beetles, the group to which I am particularly referring below. It is characteristic of the boreo-Alpine species—at any rate in typical cases —that one and the same species has two well separated areas of distribution, one in northern Europe and one in the Alpine range of folded mountains or in the adjacent mountainous areas; they are, however, absent from the intermediate lowlands: northern Germany, Poland, Denmark, etc., at any rate as continuous populations. A thorougher analysis shows, however, that the boreo-Alpine fauna should rather be regarded as a European-Atlantic marginal fauna, whose distribution extends from Fennoscandia, across Iceland, Greenland, the North Atlantic minor islands, and northern Great Britain, whence there is a great gap to the occurrences in the Pyrenees and the central European mountainous regions. Hardly any species is found in all the areas mentioned; many are boreo-Alpine in the actual meaning of the word, others are boreo-British, some are exclusively Nordic, and the rest of them are species indigenous to high mountains in larger or smaller areas of the Alpine landscapes.

For our understanding of the age of the particular species and the alterations (or absence of alterations) of the demands they make on their surroundings and of their morphology which have taken place in the course of years, it is of great interest to elucidate the trends along which this special fauna developed. Among other things, it is of importance in a valuation of the Baltic amber fauna

as compared with the fauna living to-day within the same geographic areas.

Precisely the beetles comprise species which according to their biology and morphology have very poor possibilities for a passive spreading over large distances, and whose abilities for an active spreading are extremely limited; this applies i.a. to the high-Nordic species of the weevil genus *Otiorrhynchus,* which is wingless and lives concealed. It is inconceivable that these species should have attained their present characteristic distribution post-glacially, as immigrated from centres of dispersal solely along the southern marginal areas of the inland ice. It must be assumed that preglacially the fauna of which these weevils are representatives, was distributed throughout the whole area, and that it survived the Ice Age in refuges along the margin of the ice, both along the actual inland ice and along the Alpine glacier.

It must be considered a fact that at the fall of the temperature during the Tertiary time an ever increasing suppression of an originally very rich fauna and flora took place, the same as lived in the "amber forests", with a continuous extinction of the least cold-resistant species and a gradually increasing concentration of the biological activity in isolated areas specially favoured by the climate, viz. the refuges. It must be assumed that an intense ecologic selection altered the dominant preferences within the surviving populations by elimination of all the thermophilous elements. This ecologic selection may, but need not, have been accompanied by a morphological selection.

Interglacially and postglacially a gradual extension of the areas of the refuges must have taken place, with an increase of the surviving species in the ecologic form (highly different from the original one) in which they now occur. To-day, therefore, many species vary from place to place, and the presence of a species cannot always be taken as an indication of a certain climate.

In addition, at the cessation of every ice age a faunal immigration from the outside took place whenever possible; in this way the "wintering" fauna was displaced to the most rigorous biotopes of the region, to which that fauna alone had acquired possibilities of existence. The present-day North European fauna differs somewhat from the Miocene fauna, which lived under similar climatic conditions, the immigrated species including not only a representation of those which were displaced southward during the Ice Age,

but also foreign species which did not formerly live in these areas. Only the last-mentioned species are not, probably, to be found as amber fossils.

Among beetles (and probably many other animal and plant groups) no undoubtedly observable new formation of species takes place in the north and central European regions to-day. In the Alpine folded mountain range and further southward, in localities in which minor populations may attain an effective isolation, however, the specific formation is even to-day lively and readily observable. If the conditions to-day are comparable to those of the past, it is most likely, therefore, that in northern and central Europe no essential renewal of the local insect fauna, apart from the selective one already mentioned, took place in the Miocene and Pliocene periods. On the other hand, there is reason to believe that a very lively formation of species was going on during the early part of the Tertiary period, when the climate varied from a subtropical to a Mediterranean one, and that this fauna has since then been subject to a constant decimation.

The fauna met with in the Baltic amber (besides in contemporary European and North American deposits of a quite different character) must be characterised as decidedly thermophilous; many fossils, e.g. the numerous termites, directly confirm this assumption. It must be expected that the fauna, like the corresponding recent faunas, was very rich in species, and it may accordingly be expected that a comparatively large number of species will be found as fossils. The probability is, therefore, that the insect fossils collected in these deposits will to a large extent differ specifically from the recent fauna of the same regions and from material derived from other fossil occurrences, notably if the geographic distance between them is great; but the possibility of the occurrence of common species is present everywhere.

List of the collection of amber-fossil arthropodes found in the Zoological Museum, Copenhagen (March 1965):

Crustacea		2
Oniscoidea	2	
Arachnida		618
Opilionida	17	
Pseudoscorpionida	8	
Araneida	310	
Acarina	283	

Myriopoda			24
Diplopoda			11
Symphyla			1
Chilopoda			12
Insecta			4454
Collembola			249
Thysanura			23
Ephemeroptera (1 larva)			6
Plecoptera			12
Blattoidea			26
Ensifera			7
Phasmoidea			1
Dermaptera			2
Isoptera			29
Psocoptera			61
Thysanoptera (a few larvae)			42
Hemiptera (several larvae)			249
Heteroptera	36	Aleyrodidae	10
Auchenorhyncha	62	Aphididae	98
Psyllidae	1	Coccidae (♂♀)	42
Neuroptera (1 larva)			5
Trichoptera (1 larva)			121
Lepidoptera (20 larvae)			47
Diptera			2445
Mycetophilidae	340	Erinniidae	6
Sciaridae	347	Tabanidae	1
Bibionidae	5	Rhagionidae	17
Trichoceridae	49	Asilidae	5
Tipulidae	3	Empididae	106
Culicidae	2	Dolichopodidae	361
Psychodidae	73	Syrphidae	9
Cecidomyiidae	83	Phoridae	104
Chironomidae ♂	268	Cyclorrhapha, undet.	24
Chironomidae ♀	403	Flies, undet.	115
Ceratopogonidae ♂	32	Diptera, undet.	3
Ceratopogonidae ♀	60	Larvae	8
Eohelea Petr. ♀	4	Pupae	2
Simuliidae	13		
Hymenoptera			693
Tenthredinidae	1	Evaniidae	2
Proctotrypidae	175	Ichneumonidae	25
Encyrtidae	10	Chrysididae	1
Chalcididae	60	Formicidae	306
Trichogrammatidae	3	Aculeata, undet.	10
Mymaridae	22	Hymenoptera, undet.	4
Braconidae	74		

Coleoptera			436
Carabidae	4	Colydiidae	8
Staphylinidae	16	Phalacridae	1
Pselaphidae	9	Cryptophagidae	6
Scydmaenidae	32	Lathridiidae	15
Silphidae	11	Mycetophagidae	18
Clambidae	2	Endomychidae	6
Corylophidae	3	Coccinellidae	2
Ptiliidae	3	Aspidiphoridae	1
Scaphidiidae	1	Ciidae	3
Cantharidae	2	Oedemeridae	1
Malachiidae	4	Pyrrhochroidae	1
Dasytidae	5	Scraptiidae	19
Cleridae	4	Aderidae	21
Eubriidae	1	Anthicidae	2
Helodidae	40	Serropalpidae	4
Anobiidae	21	Anaspidae	13
Ptinidae	3	Mordellidae	14
Bostrychidae	2	Lagriidae	2
Elateridae	35	Alleculidae	1
Throscidae	5	Tenebrionidae	3
Buprestidae	1	Cerambycidae	3
Byrrhidae	3	Chrysomelidae	8
Dermestidae	4	Anthribidae	1
Ostomidae	1	Curculionidae	7
Nitidulidae	3	Ipidae	11
Cucujidae	1	Coleoptera, undet.	8
Erotylidae	3	Larvae	36

Publications based, at least partially, on the Copenhagen amber collection:

Demoulin, G., 1965: Contribution à la connaissance des Ephéméroptères de l'ambre oligocéne de la Baltique. — Entom. Medd. 34 p. 143-153.

Hennig, W., 1965: Die Acalyptratae des Baltischen Bernsteins und ihre Bedeutung für die Erforschung der phylogenetischen Entwicklung dieser Dipterengruppe. — Stuttgart. Beitr. Naturk. 142.

Larsson, S v. G., 1962: The Copenhagen collections of amber fossils. — Entom. Medd. 31 p. 323-326.

Petrunkevitch, Alexander: 1957: *Eohelea stridulans,* n. gen., n. sp., a striking example of paramorphism in an amber biting-midge. — Journ. Paleont. 31 (1) p. 208-214.

—, 1958: Amber spiders in European collections. — Trans. Conn. Acad. Arts Sci. 41 p. 97-400.

In preparation:

C a r p e n t e r, F. M.: Neuroptera.

Cr o w s o n, R o y A.: Cleroidea.

H e i e, O l e: Aphididae.

H e n n i g, W.: Cyclorrhapha (excl. Syrphidae, Phoridae and Pipunculidae).

I l l i e s, I.: Plecoptera.

P a r k, O r l a n d o: Pselaphidae.

R e m i n g t o n, C h. L.: Thysanura.

S u t e r, W.: Scydmaenidae.