Palaeobiology and mode of burial of the insects of the Lower Eocene Mo-clay of Denmark

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Insects are preserved in the Mo-clay mainly at two distinct horizons. These insect assemblages are large and important; in composition they contrast strongly with the better known, more or less contemporaneous Baltic amber faunas. The palaeobiology of the two Mo-clay assemblages and their mode of burial are considered. Both assemblages indicate an origin in a fauna or mixture of faunas in a landscape near the Scandinavian coast of the Mo-clay sea, dominated by meadows and scrub, and free of true forests. Considerable differences in the make up of the two assemblages are attributed to different times of year when the insects were transported offshore. Both assemblages comprise heavy-flying insects and lack strong flyers, small insects and flightless forms. This is considered to indicate that transport from land was by storm winds, not by water. The burial of well preserved insects mainly at two levels is attributed to a combination of catastrophes: storm winds blowing from land, and reduction of marine fauna, either by 'red tide' mass mortalities or volcanic ash falls. A report is presented of the material of 1800 specimens in the Geological Museum, Copenhagen, and Fur Museum, Jylland, Denmark, but a detailed taxonomic study remains to be made.

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The Mo-clay is a 50–60 m thick diatomite that crops out chiefly in the western Limfjord area of NW Jylland, Denmark, with the islands of Fur and northern Mors as its centre (Sorgenfrei 1957). The rock is highly porous and has a very low density. Its colour is grey when wet, drying to yellowish white. Characteristic of the Mo-clay is its content of volcanic ash, which is distributed as about 200 layers within it (Bøggild 1918; Gry 1940, 1964). The ash originated from a volcanic area that is believed to have been located in Skagerrak (Sharma 1970; Flodén 1973). Many individual ash layers are sufficiently distinctive that they can be correlated between sections, and on this basis a stratigraphy of the layers has been established (fig. 1). The rather closely spaced ash layers in the upper 20 m have been numbered from + 1 upwards to + 140, while the much less frequent ash layers in the lower more than 30 m have been numbered downwards from – 1 to – 39. The numbered layers are generally over ½ cm thick (maximum c. 20 cm); traces of much thinner ash layers can often be found in between them. Individual ash layers are normally graded, with a sharp base and coarse material at the bottom, fining upwards and passing gradually into the overlying diatomite.

Between the ash layers the sediment is finely laminated with alternating lighter and darker layers 1–2 mm thick. Bonde (1973, 1974) has recently discussed the palaeo-oceanography, -geography and -climatology of the formation. Bonde considered it possible that these structures were annual varves consisting of a summer and winter zone, which led him to estimate the total duration of the period of Mo-clay deposition to be c. 60,000 years. In contrast, Sharma (1969) arrived at a figure of c. 3 million years for this period on the basis of magnetic reversals recorded in the series of ash layers. This lamination is obscured locally by short intervals of a more homogeneous sediment which Bonde (1973, 1974) considered to be caused by bioturbation of a sparse benthic fauna.

At certain horizons, calcium carbonate cement has produced well lithified layers of 'cementstone'. These cemented layers occur pre-

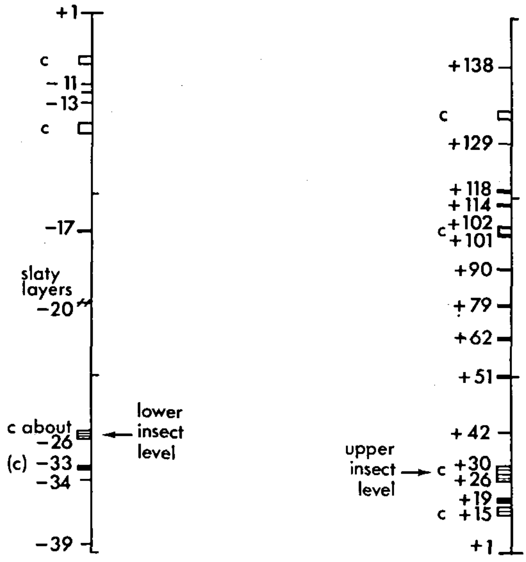


Fig. 1. Idealized section of the 'Mo-clay Formation' (after Bonde). The more important ash layers are indicated by their numbers. Cementstone levels are indicated by c. Vertical scale marked in 10 m intervals.

dominantly at certain levels, as described by Bøggild (1918, p. 44). (1) About 1 m above ash-layer + 130 a row of cementstone concretions occurs without any enclosed ash layers. (2) Ash-layers + 101 and + 102 are nearly always incorporated in a single cementstone bed with the diatomite between them. (3) Ash-layers from c. + 25 to + 30 most commonly are included in a row of large and characteristic concretions. (4) An ash-free concretion horizon occurs somewhere between + 1 and − 11. (5) A few hard cemented layers at c. − 20 (Bøggild 1918, p. 45) are according to Gry (1940) siliceous slaty layers.

In addition to these five levels recognised by Bøggild (1918) two additional levels occur in many localities, one between (3) and (4) at + 15 and another a little below − 13. In some of these concretions insect remains are rather common (Bonde, pers. communication).

Furthermore, Andersen (1947, p. 189) found loose blocks of a characteristically striped cementstone at Ærtebølle in the overlying moraine or washed out on the shore. Recently, M. Breiner has found the striped cementstone in situ in the oldest layers of the Mo-clay series in Knudeklint, Fur, between − 21 and − 29 (Pedersen 1960).

Finally, concretions occur also in − 33 at Knudeklint, Fur, and have yielded a nearly complete skeleton of a leatherback turtle, *Eosphargis breineri* (Nielsen 1959).

Reconstruction of environment

Bonde (1973, 1974) has reconstructed the palaeographical and -oceanographical setting of the Mo-clay deposits on the basis of upwelling currents (fig. 2), an assumed distance of 100 km from the coast and an approximate water depth of a few hundred metres. Offshore winds produced upwelling which caused enrichment of surface waters with nutrients, planktic blooms and depletion of oxygen, causing in turn a reduction of the benthic community. This model explains the production of a diatomite with many fish but with little or no bioturbation, and having a rich terrestrial fauna. Lack of calcareous skeleta is probably secondary, due to dissolution by slightly acidic stagnant bottom waters.

Of the terrestrial fauna preserved in the Mo-clay it is remarkable that all avian bones

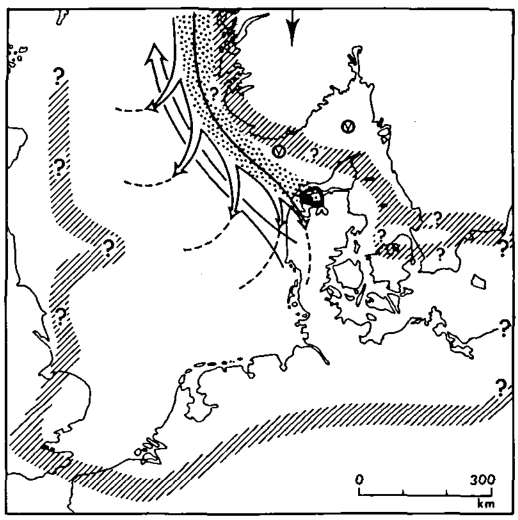


Fig. 2. Model of the palaeogeography and -oceanography of the 'North Sea' while the Mo-clay was deposited (after Bonde 1974). Approximate position of coast line shaded. The Mo-clay area is encircled by a thick line. v indicates possible volcanic centers. Prevailing northerly winds are indicated by an arrow. Surface current southwards producing upwelling (stipled) and its subsurface countercurrent are indicated.

identified belong to land birds (Hoch in press).

The plant fossils

Large collections of land plant fossils are housed in the Mineralogical Museum, Copenhagen, and in the Fur Museum. Koch (1960, p. 283) mentions a leaf which is probably from *Salvinia,* a cone of *Pinus* cf. *Laricio thomasiana* and a leaf of *Ginkgo* cf. *adiantoides.* Moreover a piece of grass apparently belongs to the bamboo group; Koch also referred, with some doubt, the grass-like leaves and jointed rhizome segments found commonly in the striped cementstone to this group. A specimen of *Macclintockia kanei* is also mentioned. According to Koch, this material bears evidence of having undergone considerable transport. Koch also states that fossil wood occurs commonly, and some specimens have well-preserved bark. The Mo-clay wood appears rarely to have been bored by shipworms (F. J. Mathiesen, pers. communication).

The jointed rhizomes mentioned above are rather slender, in their flattened condition hardly over 5–6 mm wide; some of them equipped with fine, well preserved, fibrous roots that just like the accompanying leaves bear indications of having been at the same time brittle and flexible in living condition. They appear to have been deposited on the sea floor in a rather fresh state and must have belonged to a riverbank flora from stagnant or slowly flowing, fresh or brackish water. The rhizomes and grass leaves have a growth type more or less resembling today's *Sparganium* or *Glyceria,* and the above mentioned sturdy, bamboo-like grasses presumably grew in a similar biotope.

In addition, an isolated leaf of *Salvinia,* which belongs to the primarily tropical water fern family, has been found in I. P. Andersen's collection (Ærtebølle, re. 381) in the Geological Museum, Copenhagen. Other plants, also flowering dicotyledons, await identification.

The remaining plant material consists first and foremost of numerous pieces of wood, chiefly of conifers, but not more closely identified. There are known in addition fascicles of pine needles, winged coniferous seeds, nuts, and occasional large, silicified pieces of trunks, of which the largest belongs to the Taxodiacea (F. J. Mathiesen, det.). To this material belong also the pieces of amber, one of which is partly enclosed in a piece of wood of the original resin-producing conifer. Leaves of *Macclintockia* are found; this extinct plant often has been referred to the Lauraceae, but Takhtajan (1969, p. 191) designated it as a "problematical organ-genus".

These considerably transported plant fragments probably derive from a wooded land where the streams have been narrower and faster than in the coastal lowland. This material probably has been carried out to sea where it sank relatively quickly to the bottom in its already waterlogged condition; this may be indicated, for example, by the absence of shipworm attack.

M. Breiner (pers. communication) has added some further observations. Like fossil insects, the plants are primarily found in the lower and upper levels of insectiferous cementstone (fig. 1), with an apparant difference in flora in the two beds. Thus, certain long pointed leaves and the sturdy grass-like leaves are found only in the upper level, whereas jointed rhizomes are known only from the lower level. Furthermore, wood fragments from this lower level have a consistency like lignite (e. g. the piece containing amber) whereas the wood from the upper level is silicified.

Two of the few pieces of amber which have been found in cementstone originate from the lower level and show that at least one species of tree which produced amber resin was able to thrive in the North Sea area in the early part of the Tertiary. This plant's systematic position is unknown. However, contemporaneous succinite has been reported from the east coast of England from Essex to Yorkshire (Conwentz 1896, p. 161) and it is likely that the same conifer, *Pinites succinifer,* was not only the source of large amounts of Baltic amber and English east coast amber, but also of part of that of the Mo-clay. However, Prof. Curt W. Beck, Vassar College, N. Y., U. S. A., has studied one of the mentioned Mo-clay amber pieces by infrared spectroscopy, and says with certainty that "the resin of the Mo-clay is not succinite or so-called Baltic amber." On the other hand the spectrum agrees "quite well with those of the large and vague group of resins that have been called retinites" (C. W. Beck, pers. communication). Thus it is clear that Danish ambers are of a complicated nature and their problems are far from solved. In the Mo-clay itself remains have been found of both Pinaceae and Taxodiaceae. It should however, be pointed out that the amber found in the London Clay, while it is of approximately the same age as the Mo-clay, originates from a member of the Burseraceae, a dicotyledon family now occurring in the tropics and subtropics, and that amber in the Rhineland predominantly seems to have come from Taxodiaceae (*Sequoia* and related forms) and dicotyledons, among which have been *Liquidambar* of the Hamamelidaceae (Langenheim 1964).

It is likely that both the fossil land animals and plants, together with the few pieces of amber from the Mo-clay, derived from the SW coast of Scandinavia some 100 km from the area of deposition (fig. 2).

Occurrence of insects

The Mo-clay as a whole is rich in macrofossils (e. g. fishes, Bonde 1966). Especially remarkable is the large number of insect fossils, which are otherwise rare from the older Tertiary. Insects occur chiefly in cementstone concretions from the levels +25 – +30 and between –21 and –29 (these levels are herein called upper and lower (insect) levels respectively). These two insect-rich layers were separated by a period of time during which some 30 m diatomite was deposited and some 60 volcanic eruptions occurred (fig. 1).

The lower cementstones are about 30 cm thick and contain at least 4 numbered ash layers; the cementstones from the upper level are about half a metre thick and many comprise as much as 7 numbered ash layers; there is as yet no evidence that the insects are confined to one or only a few horizons (bedding planes) within the two levels (Bonde, pers. communication). As mentioned above, other cementstone levels between the upper and lower also contain insects, but they are not well recorded in the collections.

The insect material

Our knowledge of the insects of the L. Tertiary is very limited and the investigation of the insects of the Mo-clay is still in its early stages. Interest in the Mo-clay insects is stimulated, however, by the considerable information they impart both on the terrestrial environment of Scandinavia and on depositional conditions in the Mo-clay sea. Further stimulus is provided by the fact that international insect palaeontology of the L. Tertiary is based largely on finds in amber, and seems unacquainted with the extensive Mo-clay fauna.

Only a few of the Mo-clay insects have been previously described, most of them by Henriksen (1922). These are: the damselfly *Phanacolestes jutlandica;* the long-horned grasshoppers *Nymphomorpha medialis* and (in 1929) *Tettigonia amoena;* the lacewing *Megalomus densistriatus;* the leaf beetle *Cassida* sp.; the ichneumon fly *Pimpla stigmata*; the crane flies *Tipula binoculata, Eriocera dimidiata* and *Rhamphidia thybotica;* the cicadas *Hammapteryx paucistriata, Eoricania danica, Ormenis furcata* and *Lechaea primigenia;* and the bugs (*Tectocoris?*) *angustilobatus, Teleoschistus multinervosus* and *Teleocydnus transitorius*. Moreover, Henriksen described several insects that are not completely identifiable.

Dr. Henriksen was an eminent entomologist but not a specialist in any of the insect groups treated here. It may therefore be expected that with reinvestigation a number of these species will be referred to other genera. Indeed, Zeuner (1936, p. 252) has already transferred the grasshopper *Tettigonia amoena* to the new genus *Pseudotettigonia* in the subfamily Tettigoniinae and of *Nymphomorpha medialis* he wrote (p. 265) that on the basis of the existing remains it is impossible to determine the species' position in the system.

The few aphids in the material were described by Heie (1967, 1971): *Siphonophoroides breineri, S. magnalata* and *Diatomyzus eocaenicus*.

In Henriksen's time the collections comprised only about 50 specimens. Today the number of fossils in the two Danish collections (Geological Museum, Copenhagen and Fur Museum) is about 1800, and moreover there is a large collection in the Palaeontological Institution in Uppsala, Sweden. Nevertheless, many of these fossils are useless for fine taxonomy and can only be used for statistical studies on the different orders of insects, and the relative fossilization potential of these orders.

A contemporary and considerable material of insect fossils from marine deposits of north Germany was mentioned by Illies (1941, 1942). This collection contains two species of Orthoptera, two Blattoidea, 17 Coleoptera, 2 Hymenoptera, 2 Odonata, 2 Neuroptera, 6 Trichoptera, 7 Diptera, 9 Heteroptera and 11 Homoptera (Illies 1941, p. 22). No species was described, but a *Megalomus* sp. (Neuroptera), a homopteran and a tipulid were figured.

Table 1 shows that the composition of the assemblages in the two insect-rich horizons is significantly different. In many cases the numbers are so small that they tell us nothing. Other drawbacks are that the horizon is only identified with reasonable certainty in about one third of the material; and that the material from the upper level is about three times larger than that from the lower level. The material is therefore insufficient for reliable statistical treatment. Nevertheless, comparison of the two located assemblages does indicate that in the lower layer there are relatively many cicadas, water bugs, damselflies and beetles, and that cicadas and beetles on the whole dominate this assemblage. In the assemblage of the upper level, on the other hand, pentatomoids, caddisflies and crane flies play a predominant role, and grasshoppers and flies are far more common here than in the lower horizon. Andersen (1947, p. 192) attempted a similar comparison of his own collections from striped cementstone (lower layer) with Henriksen's published information, and on the basis of this much less substantial material arrived at a comparable result: "striped cementstone differs from typical cementstone in that it contains *many more beetles and fewer bugs*" (translation). According to Andersen, the striped cementstone also contains many more plant fragments than other horizons.

It is doubtful whether valid conclusions may

Table 1. Survey of the known insect fossils in Danish Mo-clay collections.

	Layers −21 to −29		Layers + 25 to + 30		Layer Unknown	Total Number
Blattoidea	0		0		2	2
Ensifera	1	(0.7 %)	17	(3.8 %)	21	39
Caelifera	1	(0.7 %)	1	(0.2 %)	11	13
Dermaptera	1	(0.7 %)	5	(1.1 %)	5	11
Auchenorrhyncha	37	(25.1 %)	87	(19.5 %)	299	423
Aphidoidea	0		5	(1.1 %)	4	9
Heteroptera	16	(10.7 %)	100	(22.4 %)	329	445
Belostomidae	0		1	(0.2 %)	0	
Gerridae	5	(3.4 %)	1	(0.2 %)	8	
Pentatomoidea	3	(2.0 %)	91	(20.4 %)	248	
Other Heteroptera	8	(5.4 %)	17	(3.8 %)	73	
Zygoptera	7	(4.8 %)	0		30	37
Anisoptera	0		0		2	2
Ephemeroptera	0		2	(0.4 %)	3	5
Plecoptera	0		0		1	1
Neuroptera	7	(4.8 %)	23	(5.1 %)	60	90
Mecoptera	0		3	(0.7 %)	6	9
Trichoptera	6	(4.1 %)	48	(10.7 %)	100	154
Lepidoptera	0		2	(0.4 %)	4	6
Nematocera	7	(4.8 %)	66	(14.8 %)	152	225
Tipuloidea	1	(0.7 %)	58	(13.0 %)	87	
Other Nematocera	6	(4.1 %)	8	(1.8 %)	15	
Brachycera	5	(3.4 %)	33	(7.4 %)	70	108
Hymenoptera	2	(1.4 %)	11	(2.5 %)	16	29
Coleoptera	29	(19.7 %)	27	(6.0 %)	93	149
Unidentified insects	28	(19.0 %)	17	(3.8 %)		45
Totals:	147		447		1208	1802

be drawn about variations in the structure and fauna of the landscape on the basis of the differences in the assemblages. It is more likely that the insects were carried out to sea by storms and that the differences reflect different times of year when the storm struck the insect community, the composition of which was continually changing with the annual biological cycle. Even under subtropical conditions each species maintains an annual periodicity and relatively constant rate of development, so that the great majority of individuals of a single species emerge more or less simultaneously. Thus only a slight difference in time may produce a considerable difference in the composition of the fauna.

There are other features of significance in the two assemblages. In the entire material not a single wingless insect is represented; nor are there any insect larvae, millipedes, arachnids or land snails. Nearly all the insects present are heavy-flying forms that have some difficulty in changing direction: these are the cicadas, bugs, caddisflies, crane flies and to some extent beetles. These groups are all with certainty overrepresented in the Mo-clay in comparison with the original composition of the fauna. Grasshoppers are only represented by a few species, which on the other hand are relatively abundant; most grasshoppers do not fly willingly. The same applies to the earwigs, cockroaches and stoneflies, which are extremely rare in the Mo-clay assemblages. The termites have only their yearly mating flight, the timing of which is rigorously controlled by weather conditions; termites do not occur in the Mo-clay at all. Among the Odonata, the damselflies are weak fliers and are relatively common while the more elegantly flying dragonflies are represented only by a few fragments. The very good fliers, the wasps and flies, are found in numbers that do not even begin to approach their presumed abundance in the fauna of the source area (as indicated by their common occurrence in amber). Typical of the Mo-clay assemblages is that small and light-weight insects are rare, even considering that they may in part have been overlooked. Small gnats and microhymenopterans, which are so overwhelmingly common in amber, are nearly completely absent. It is thus quite clear that the Mo-clay assemblage is the result of selective sorting by mechanical processes.

Since the Mo-clay assemblage consists exclusively of winged individuals it is clear that it has been carried out to sea by air currents and not, as with the plants, by water currents. Furthermore, since the assemblage is exclusively composed of larger, heavy-flying insects that usually spend only short periods of time in flight, it must be concluded that they derive from the nearby coastal areas, which must necessarily be Scandinavia's southwest coast. The offshore wind must have been sufficiently strong to drive the vegatation-bound bugs and cicadas to flight. Stronger fliers such as dragonflies, many Lepidoptera and others were either able to withstand the wind pressure or were carried farther away. Very small insects especially are easily incorporated in air plankton and may be carried enormous distances.

Involuntary wind transport of insects out over the sea can also be observed today but in our latitudes, at least, they have little chance to be deposited on the sea bottom. Such seems also to have been normally the case along the coast of the Mo-clay sea; usually the drowned insects will have fallen prey to surface fish and other carnivores. But exceptional conditions appear to have reigned at certain periods, during which the insects have remained uneaten and have sunk slowly to the sea floor of diatom ooze, where they have also escaped the attentions of the very few benthic animals. Although the air-filled insects must have sunk slowly to the bottom, they have not been subject to much decay; the cuticular plates of the body are most commonly in exemplary condition and even completely preserved skeletons are found. In most cases, however, the wings have become detached before burial.

The reason for the insects reaching the sea floor in so undamaged a condition may possibly be sought in a contemporaneous mass mortality of fish, or in an episode with reduced numbers of fish, with a simultaneous lack of benthic scavengers. Bonde (1966, p. 201) wrote: "Undisturbed bedding-planes, well preserved fossils, rarity of bottom living invertebrates, and lack of real bottom-fishes indicate stagnant, maybe even poisonous water at the bottom. Mass mortality of fishes may occur in some horizons" (see also Bonde 1974, p. 31).

If mass mortalities occurred in the Mo-clay sea, they were probably brought about by the excessive bloom of pelagic dinoflagellates, known in modern tropical seas by the name 'red tide'. These mass mortalities are caused by the dinoflagellates (e. g. of the genera *Gonyaulax* and *Gymnodinium*) out-competing the diatoms by virtue of their smaller requirements for food and light. This disrupts the food chains since dinoflagellates are poorly suited as food for copepods, and ultimately the first population becomes reduced. Moreover, the dinoflagellates secrete toxic substances, and where the bloom is dense, these toxins prove fatal to nearly all life in the area (Thorson, 1961, p. 29). Direct evidence of 'red tide' conditions in the form of preserved dinoflagellate skeletons has not been found. Neither have bedding-planes been found covered with large numbers of perfectly preserved fish and insects, that would constitute direct evidence of mass mortalities. However, the general setting envisaged by Bonde (1973, 1974) with upwelling water and offshore winds is ideally suited to this type of plankton bloom.

Another possible cause of mass mortalities may be connected with volcanic eruptions. A rain of ashes onto the sea might disturb the physico-chemical balance of the ecosystem. If this disturbance should adversely affect the diatoms the dinoflagellates might explode in a 'red tide' bloom. Again, however, no direct evidence is available to support this hypothesis.

In conclusion, then, it may be envisaged that from time to time offshore storm-winds have carried numbers of insects to sea, drowning the heavier fliers selectively not too far off the coast where the Mo-clay was being deposited. Under normal conditions the drowned insects would have been rapidly consumed by the marine fauna, no doubt mostly the surface fish, so that insects were normally not preserved in the sea floor. The few insect-rich horizons are considered to be the result of the rare combination of an insect-laden offshore wind and a 'red tide' mass mortality in the sea, effectively killing off the scavengers that normally destroyed the insect corpses. Under these conditions the dead insects sank slowly and unmolested to the bottom and were incorporated, tolerably undamaged, in the accumulating sediments.

Report on the Mo-clay insects in the Geological Museum in Copenhagen and Fur Museum

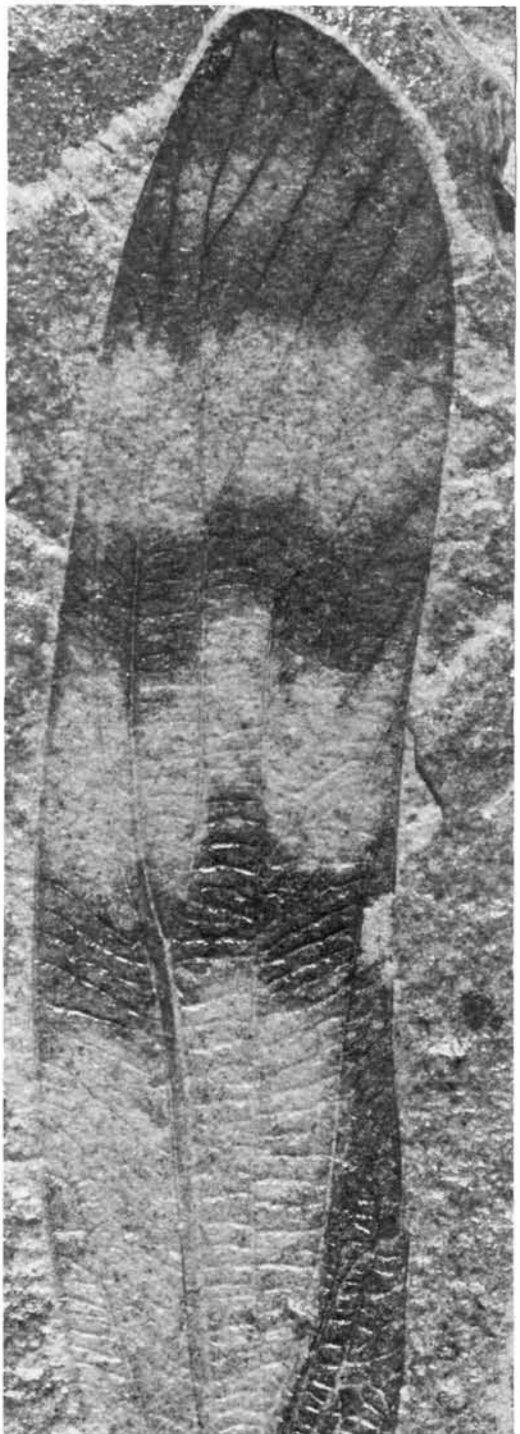
As already mentioned, only very few of the Mo-clay insects have been studied scientifically, and much specialist work still remains. It is therefore not possible to give as detailed an analysis of the material as can be done with insects preserved in amber.

Blattoidea

The cockroaches are known only from two specimens, both forewings, one at Copenhagen and one at Fur. As the open coastal plain probably has provided this order with a less satisfactory environment than the woodlands behind it, and as cockroaches moreover are poor fliers that do not fly willingly, one could not expect them to occur with greater frequency.

Saltatoria

Of grasshoppers are found both long-horned and short-horned families (Ensifera and Caelifera). *Tettigonia amoena* Henriksen is by far the most common species; it is the size of a large present-day *Decticus verrucosa* and is characterized by the dark cross-bands on the forewings (fig. 3). The material comprises first and foremost loose wings, but there are also hind legs that, according to their size, may belong to the species; there is an impression of an abdomen, where the profile of the female's ovipositor is clear to the smallest detail; and there is a fragment of the basal part of a forewing with the entire venation of the males' stridulatory organ clearly reproduced. Whether all these details actually belong to the same species, however, can only be determined by a specialist. The species seems exclusively to belong to the horizon + 25 to + 30. Long-horned grasshoppers are also represented by



isolated uniformly coloured fragments of wings, among these *Nymphomorpha medialis* Henriksen. Of short-horned grasshoppers the material contains a smaller number of impressions of usually length-wise-folded wings. All the mentioned grasshoppers seem to belong to the fauna of the open land.

In I. P. Andersen's material (Geological Museum) there is a slab (no. 415) with c. 12 insect eggs, in all probability grasshopper eggs. They are c. 0.75 mm long, arranged haphazardly but close together on and in a structureless, dark, "soft" material (monocotyledonous plant material). This is very likely the only water-transported insect material in the Mo-clay.

Dermaptera

The earwigs are only sparsely represented; there are about a dozen males and females which possibly belong to a single species. The pieces are generally unsuitable for study. In some instances the impressions are only partly exposed, so there is hope that careful preparation can bring the most important details to light.

Auchenorrhyncha

Many cicadas, especially wings of such, are well preserved and suitable for study. Others cannot even be identified to family and are only of use in forming an estimate of the order's relative frequency in the material. There are many animals in both of the insect-bearing horizons, although they seem to have a relatively greater frequency in the lower level. The Mo-clay collections in all contain more than 400 specimens. There are dominating species among them, but moreover the number of species is large, and the material is distributed among several families. It mainly comprises large and medium-sized species (fig. 4).

Fulgoroidea play a large role; the large-winged families Ricaniidae and Flatidae are richly represented, and this applies even more to the Cixiidae. These forms are more likely to use their wings than most of the other cicadas, which is probably why they are so frequent in

Fig. 3. Tettigonia amoena *Henriksen. Forewing of female. Length about 60 mm. Fur Museum.*

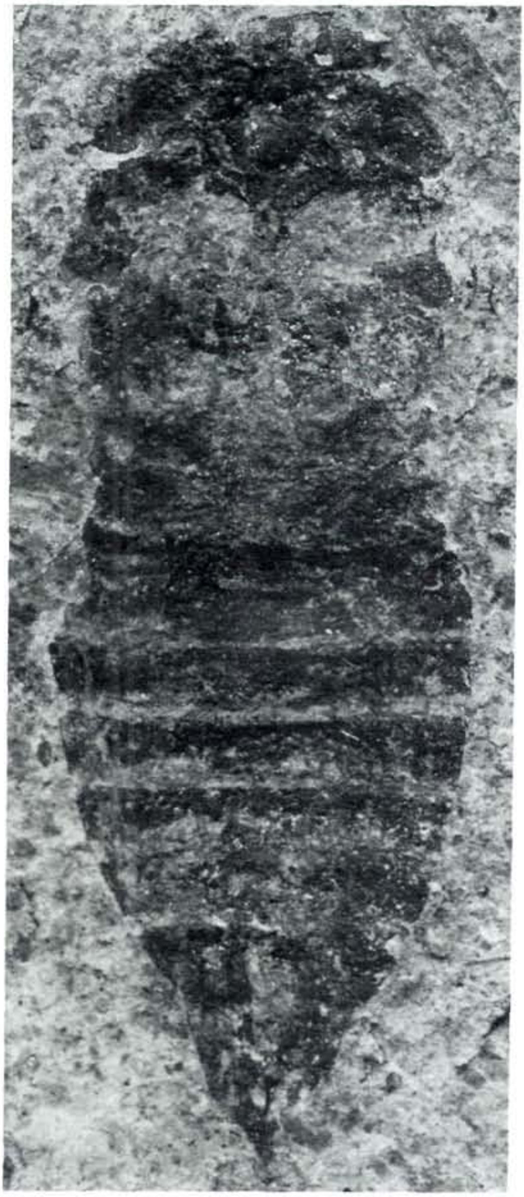


Fig. 4. Ventral side of undetermined cicada, family Cicadidae. Wings lost. Body length c. 32 mm. Fur Museum.

the Mo-clay. Smaller cicadas are also found in the Mo-clay, among which a number seem to be Cercopidae and a few Issidae. Among the larger individuals are specimens of the family Cicadidae. It is characteristic that the Mo-clay cicadas are generally larger than the amber cicadas.

Only an insignificant part of this large fossil material from the European Eocene has been worked up: *Hammapteryx paucistriata, Eoricania danica, Ormenis furcata* and *Lechaea primigenia,* all described by Henriksen (1922). The cicadas seem to be one of the most interesting orders of insects that occur in the Mo-clay.

Aphidoidea

Aphids are rare in the Mo-clay and mainly represented by species of the genus *Siphonophoroides* (Callaphididae), which is also known from the Oligocene Florissant-layer in North America (Heie 1967, p. 208; 1970, p. 166). As aphids are very common in air plankton and often are carried over very long distances by the wind, the place of origin of these Mo-clay aphids remains unknown. As they belong to a group that today lives on maple and other deciduous trees, it is more likely that they have come from a more distant woodland than from the apparently sparsely wooded coast. In 1970 (p. 163) Heie described the aphidid *Diatomyzus eocaenicus.* As both Callaphididae and Aphididae are distinctly boreal families it seems most probable that all the mentioned aphids were transported over long distances before they drowned in the Mo-clay sea.

Heteroptera

Three dominating species of bugs have been described by K. L. Henriksen (1922): (*Tectocoris?*) *angustilobatus* (Scutelleridae), *Teleoschistus multinervosus* (Pentatomidae) and *Teleocydnus transitorius* (Cydnidae). The descriptions are based on rather unsatisfactory material. Today the Danish Mo-clay collections include more than 400 bugs, of which c. 70 % belong to the above-named three families. A very few species dominate and occur in such large numbers that it must be possible to work out nearly complete descriptions on the basis of a larger number of specimens. Most of the Mo-clay's pentatomoids have lost their wings, but many of the loose wings may be identified with the help of the comparatively few that are still attached to the insects. The pentatomoids are very dominant in the upper insect horizon but evidently play a very small role in the lower horizon.

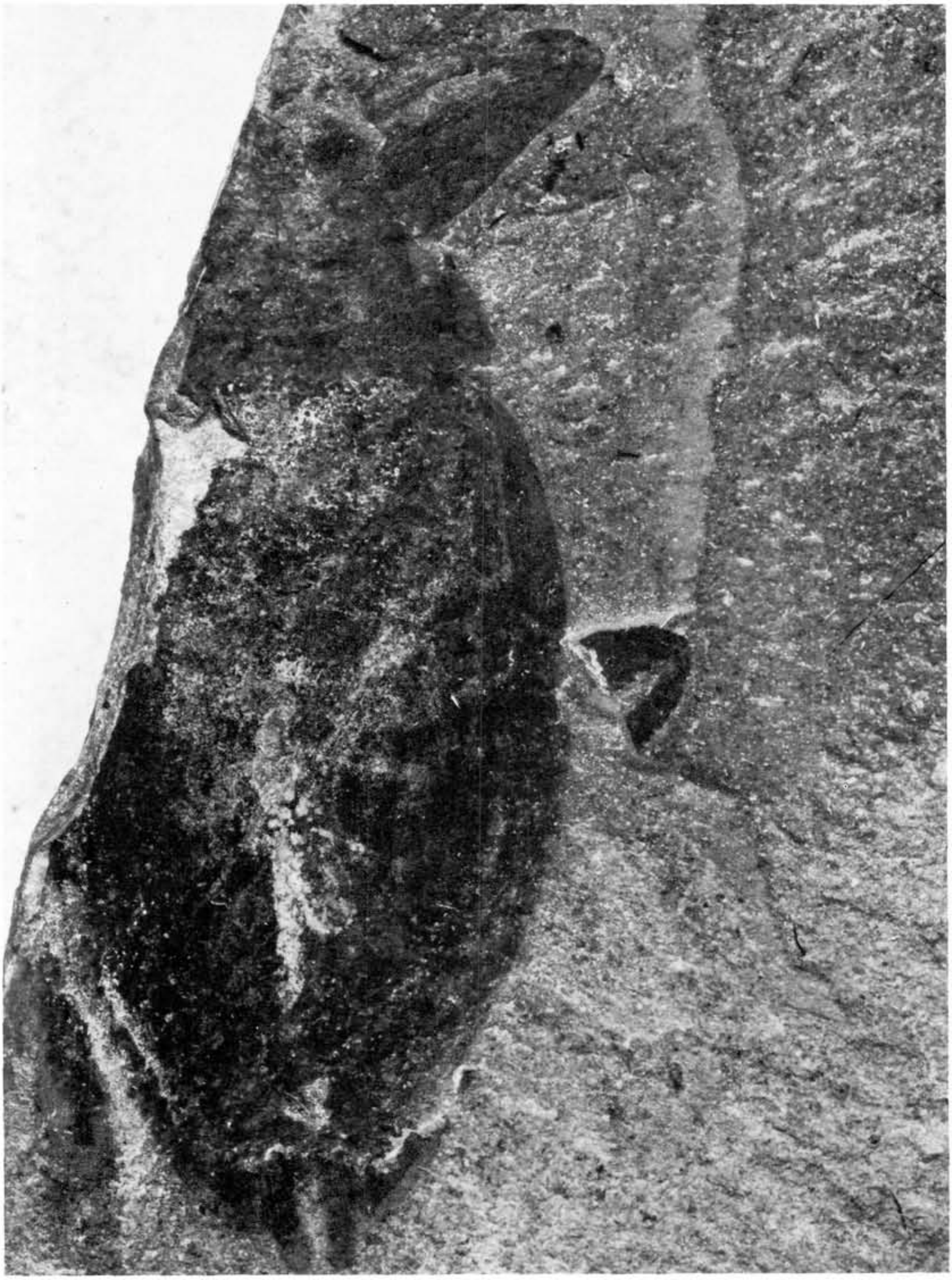


Fig. 5. Undescribed water bug of the family Belostomidae. Length c. 38 mm. Fur Museum.

The rest of the real land bugs are distributed among other families, including the Lygaeidae. The impressions of these bugs in the cementstone are generally quite faint. They seem to occur more or less evenly distributed in the Mo-clay's two insect-bearing horizons. In addition, a smaller number of water striders (Gerridae) are found, among which a very large species dominates. These are by far most frequent in the lower horizon. A water bug of the thermophilous family Belostomidae (fig. 5) has been found in the upper horizon at Fur Østklint (Fur Museum, no. 801). The occurrence of these genera seems to be purely accidental, and the possibility that they have ended up in the sea by means of water routes cannot be overlooked; a number of the water striders have been taken in blocks together with the jointed rhizomes with fibrous roots, which also belong to the lower level.

Odonata

39 fossils from this order are at present known from the Danish collections of the Mo-clay, some of which, however, are only unidentifiable fragments. This material is on the whole not worked up; only a single piece, an agrionid, has been described under the name *Phenacolestes jutlandica* Henriksen (1922). The fossil odonates from the Mo-clay are remarkable in that only two fragments come from dragonfly wings, while the remaining 37 specimens are all damselflies, among which the Calloptergyidae and Agrionidae seem to be nearly equally represented. Since we know 18 species of Zygoptera against 43 species of Anisoptera from the lignite deposits from Roth at Siebengebirge (late Oligocene) and from Öningen (Miocene) (Handlirsch 1908), the distribution of these groups in the Mo-clay is especially striking.

As previously mentioned, this distribution in the Mo-clay is doubtless due to the damselflies' weak flight in brief periods together with the special conditions that have been prevalent at the time of deposition in the Mo-clay sea. The relative abundance of callopterygids may be attributed to the Mo-clay insects, having first and foremost come from a lowland between the forest and the coast, where quiet streams and rivers, which are the preferred biotopes of many of these damselflies, have played a significant role in the landscape.

Seven of the fossils are stratigraphically localized, and it is remarkable that all these belong to the lower insect-bearing layer.

Ephemeroptera

Mayflies are very rare in the Mo-clay, a fact that doubtless has its most important basis in the individuals' very short existence as imagines. We have only five specimens, some of them too poorly preserved for definite identification. Two specimens lie close together in a slab from the upper fossil layer.

Plecoptera

Stoneflies fly very little; moreover they preferably live at rapidly flowing streams. In the light of the palaeoenvironmental model offered here, it is quite natural that we only know a single specimen (a forewing) of this insect order.

Neuroptera

The lacewings are relatively common in the Mo-clay. In Danish collections c. 90 specimens from different families are known; they are generally well preserved and suitable for study. In nearly all cases there are only loose wings, and only in isolated instances is there also an impression of the body (fig. 6). The percentage of lacewings seems to be about the same in the two insect-bearing horizons.

Only *Megalomus densistriatus* Henriksen (1922) has been described. The genus, which also has living representatives, belongs to the family Hemerobiidae and seems to be rather common in the Mo-clay material.

Mecoptera

The few scorpionflies which are known from the Mo-clay are generally well preserved. There seem to be several species, some with and some without dark wing spots. Scorpionflies are only known from the uppermost insect-bearing horizon.

Trichoptera

More than 150 specimens of caddisflies are known, but with the exception of a very few they are poorly preserved. The delicate wings,

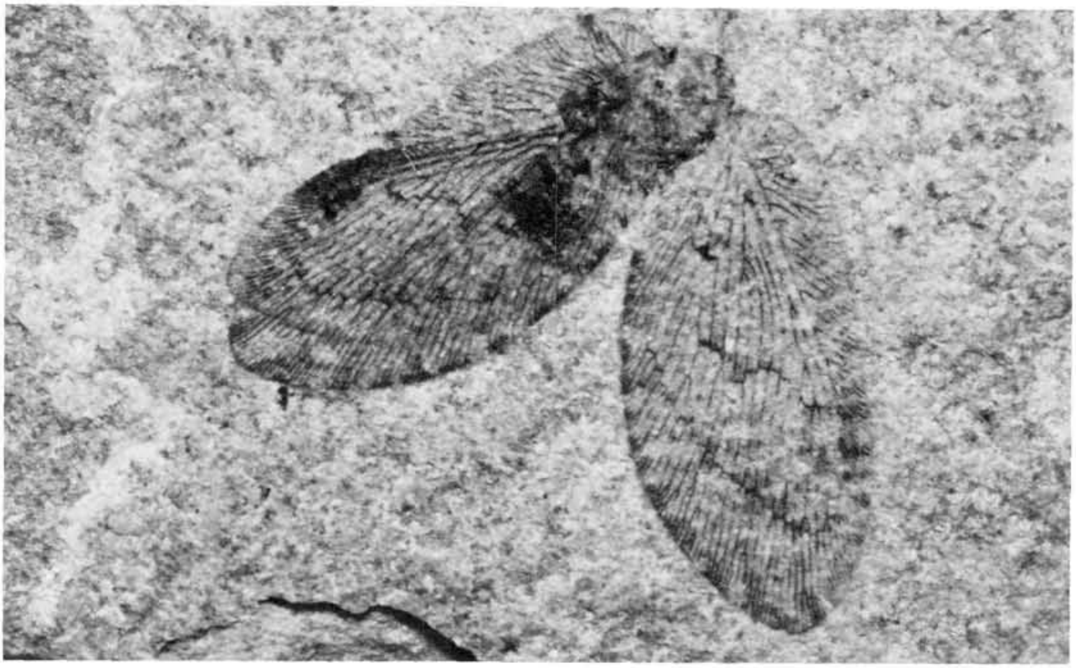


Fig. 6. One of the smaller lacewings (wing length c. 6 mm); most of the species are considerably larger. Fur Museum.

which often are rolled around the abdomen, are difficult to observe against the often somewhat rough surface of the cementstone. The best pieces are found among the detached forewings. The body is often quite accessible, and this is also true of the head with antennae and palps and of the spur-bearing legs.

The caddisflies in the Mo-clay are generally larger than the amber forms, and the balance between the different families has probably been different. One would expect a greater proportion of the forms that lived in stagnant or quietly flowing water, and fewer stream forms, which presumably would mean a larger percent of case-building species. This opens the possibility that the family Limnophilidae may be represented in the Mo-clay. One of the problems connected with the understanding of the amber fauna is that this caddisfly family, which today is the dominating family outside the tropics, is completely lacking, while representatives of all the rest of recent families are present (Ulmer 1912).

The caddisflies are relatively rare in the lower insect-bearing horizon, but are one of the dominating groups in the upper.

Lepidoptera

These are known from only a few specimens; all consist of large, detached wings with clear venation. They probably belong to the Rhopalocera.

Nematocera

The crane flies comprise more than 85 % of the Mo-clay's many nematocerans. Most belong to the family Tipulidae, but there are also a number belonging to the Limoniidae. The latter family is, however, much more poorly represented here than in amber. Most of the fossils are only wings, many in excellent preservation; in a number of instances the body is also present, sometimes also the head in a quite usable impression.

The crane flies have in 59 cases been localized stratigraphically; 58 of these come from the upper level and only one comes from the lower level.

In addition are found a number of smaller nematocerans from different families, among them the Mycetophilidae. These smaller forms have a greater relative frequency in the lower layers than is the case with the crane

Fig. 7. An extremely well preserved mosquito (Culicidae). Only very few culicids are known from the Mo-clay, and blood-sucking mosquitos are completely missing in the contemporaneous Baltic amber. Body length c. 5 mm. Fur Museum.

flies (6 in the lower against 8 in the upper = c. 4.1 % against 1.8 %). Especially noteworthy are the part and counterpart of a well preserved female mosquito (Culicoidea): important parts of body, wings, legs, head and proboscis are visible (Fur Museum, no. 340, fig. 7).

It is characteristic that it is the large, heavy crane flies, hatched in meadows and similar biotopes, that are so frequent in the Mo-clay, while other nematocerans are relatively few in number. Very likely their actual relative numbers were approximately the same as today in corresponding localities.

Single tipulids have been described by Henriksen (1922): *Tipula binoculata, Eriocera dimidiata* and *Rhamphidia thybotica.*

Brachycera

Slightly over 100 flies are known from the Mo-clay, and of these about twice as many from the younger horizon as from the older. Most specimens consist of a body with head and well-preserved, outspread wings, but loose wings are also common. In many cases the eyes, antennae and body bristles are relatively well preserved. Several recent families are recognizable: Syrphidae, Dolichopodidae, Phoridae and Empididae. A beautiful specimen of the Asilidae (fig. 8) is privately owned.

Coleoptera

About 150 specimens of beetles are known. The fossils most often consist of elytra, singly or in pairs, but in some instances we have the impression of nearly entire animals. The fossils are as such well preserved, but their structure often makes them difficult to evaluate, at times even to recognize, against the granular surface of the cementstone. Curculionidae and Carabidae seem to be frequent, and some of the wings must probably be attributed to the heteromerous families. There is a single specimen of the Chrysomelidae (*Cassida* sp.) and a relatively large water beetle (Dytiscidae), both nearly complete.

56 of the beetles can be located stratigraphically; of these 29 occur in the lower layer while 27 come from the upper layers. This corresponds to about 20 % beetles in the older horizon against nearly 6 % in the younger. Andersen (1947) already concluded from his and Henriksen's far smaller numbers that the fauna in the striped cementstone (lower horizon) was remarkably rich in beetles, and that it thus came from wooded areas as opposed to a "bug-rich" steppe fauna in the upper layers. However, the beetles found are indicative of steppe rather than forest biotopes. As previously stated, the differences between the two horizons presumably are due to accidental meteorological and seasonal conditions.

Hymenoptera

Members of this order are rather rare in the Mo-clay; 29 are known, presumably all ichneumon flies. The Brachonoidea seem to dominate; *Pimpla stigmata* was described by Henriksen (1922) together with an unidentifiable proctotrupid. The specimens are mostly well preserved, with outstretched wings fastened to the body.

Conclusions

1. The two Mo-clay insect assemblages are evidently only a part of the original faunas from which they are derived.

2. The composition of these assemblages indicates physical processes of sorting, probably involving transport by offshore storm winds.

3. From the present material it is not clear whether the insects are derived from a single fauna or are mixtures of parts of several distinct faunas brought together from different places. The apparently rather extensive differences between the assemblages of the upper and lower levels may indicate, however, that more than one fauna is represented.

4. The upper assemblage is markedly dominated by pentatomoid bugs (20.4 %), cicadas (19.5 %), crane flies (13.0 %, most Tipulidae) and caddisflies (10.7 %). Less important are flies (7.4 %), beetles (6.0 %), lacewings (5.1 %) and long-horned grasshoppers (3.8 %). Apparently this represents a fauna that may have originated from a single area, dominated by extensive meadows (Tipulidae) more or less covered with shrubby vegetation (pentatomoids, cicadas and long-

Fig. 8. Undescribed robber fly (family: Asilidae). Body length c. 12 mm. The specimen is unique.

horned grasshoppers), but lacking true forest. In this way the assemblage contrasts with the almost contemporary amber fauna. The landscape must also have been rich in stagnant and slowly flowing waters (the large number of caddisflies and limoniid crane flies). Beetles, flies and lacewings cannot be used in evaluating the biotope until they have been investigated taxonomically.

5. The lower assemblage is also dominated by cicadas (25.1 %) while pentatomoid bugs constitute only 2 %. Beetles are common (19.7

%) but of less importance are other bugs than Pentatomoidea (8.8 %, of which 3.4 % are Gerridae), damselflies (4.8 %), lacewings (4.8 %) caddisflies (4.1 %) and other Nematocera than Tipuloidea (4.1 %). The crane flies are represented by only 0.7 % as also are the long-horned grasshoppers.

6. It is remarkable that, despite the considerable differences in composition of the two assemblages (table 1), they appear to indicate comparable life conditions for the original faunas. In recent faunas, the Pentatomoidea winter as eggs, and flying adults do not emerge before rather late summer. The same is the case for at least the dominating grasshopper species. The caddisflies and crane flies winter as larvae, adults (especially crane flies) appearing in increasingly large numbers as the summer progresses. Gerridae winter as adults, appearing early in spring. The majority of beetles winter as adults, becoming fewer throughout the summer. Cicadas winter in a variety of different stages, predominantly as eggs. Therefore, the differences in the assemblages, involving particularly the bugs, caddisflies, crane flies, beetles and grasshoppers, may be explained by a difference of merely a few weeks in the time of year that the storms swept the insects out to sea. The lower assemblage appears to be earlier in the year than the upper.

7. Thus the Mo-clay assemblages are dominated by relatively large, heavy-flying insects that could hardly be transported very far before they landed on the surface of the sea. (After landing, however, such insects can be transported some distance before sinking, owing to their great content of air.) Very good flyers are underrepresented. Wingless forms and larvae are completely lacking, strongly suggesting wind transport to the sea as opposed to transport by rivers. Small, winged insects are also strongly underrepresented; such insects can easily be incorporated in high altitude air plankton and then may be transported over great distances. The few aphids possibly belong to this category and may not be derived from the same fauna(s) as the rest of the Mo-clay insects.

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Dansk sammendrag

Samlingerne af Molér-fossiler i Geologisk Museum, København og i Fur Museum indeholder over 1800 insekter (Henriksens beskrivelser (1922, 1929) omfattende mindre end 50 fund; en stor samling i Uppsala er ikke gennemgået). Insekterne er bevaret i cementsten, og særlig rige niveauer synes at være den 'stribede cementsten' (Andersen 1947), som findes i Molér-afsnittet mellem askelag −21 og −29 (nedre horisont) og den cementsten, der indeholder askelagene fra ca. + 25 − + 30 (øvre horisont). Fig. 1 viser cementstenenes placering i Moléret. Dog findes insekter også i cementsten mellem disse to horisonter. Ca. 150 vides at komme fra nedre horisont, og ca. 450 er fundet i den øvre, mens resten er uden nærmere angivelser.

Alle insektresterne er af vingede stadier, og næsten alle kan betegnes som ret store, tungt-flyvende insekter, mens virkelig gode flyvere og meget små insekter er stærkt underrepræsenteret. Dette viser, at transporten af dette terrestriske faunaelement ud i 'Molér-havet' er foregået ved vindens hjælp. Sandsynligvis er insekterne bragt ud med storme fra den skandinaviske sydvestkyst omkring 100 km borte (fig. 2), og kun de ret tunge flyvere er landet i havet så relativ nær kysten.

Tabel 1 viser hvilke insektgrupper, der er repræsenteret i Moléret og deres %-vise fordeling i de to insekt-rige horisonter. Grupperne er fra oven nedefter: Kakerlakker, løvgræshopper, markgræshopper, ørentviste, cikader, bladlus, tæger (herunder belostomider, damtæger, stinktæger, o. a. tæger), vandnymfer, storguldsmede, døgnfluer, slørvinger, netvingede, skorpionfluer, vårfluer, sommerfugle, myg (herunder stankelben), fluer, årevingede og biller.

I forbindelse med den palæo-oceanografiske model for Molér-området udarbejdet af Bonde (1973, 1974, se fig. 2) kan den usædvanlige forekomst af mange velbevarede insekter i et marint, ikke helt kystnært miljø forklares. Sandsynligvis har dinoflagellat-masseopblomstring ('red tide') været ret almindelig i det på grund af 'upwelling' meget plankton-rige overfladevand, således at fiskene (o. a. rovdyr) dér periodevis er blevet forgiftet; herved har insekter uhindret kunnet synke til bunds efter fralandsstormene. Muligvis kan også vulkanisk askeregn have spillet en rolle ved periodisk udryddelse af overfladefaunaen − bundfaunaen er i Bondes model under alle omstændigheder meget fattig eller mangler helt (hvad man bl. a. kan se af sedimentets fine laminering − varv?). Samtidig massedød af fisk og insekter kan dog ikke direkte erkendes gennem fossilfundene.

Den markante forskel, der er i hyppigheden af de forskellige insektgrupper i den nedre og øvre horisont, kan næppe med sikkerhed tydes som væsentlige forskelle i faunaerne og dermed i det terrestriske miljø. Den øvre horisont domineres af stinktæger, cikader, stankelben og vårfluer, mens den nedre særlig præges af cikader og biller.

Begge horisonters fund synes at være repræsentanter fra et område med engstrækninger med langsomme vandløb og stillestående vand og med krat og buskvækst, mens egentlige skovområder ikke kan erkendes.

De få bladlus kan måske være tilført som luftplankton fra helt andre områder.

Forskellen på de to horisonter kan muligvis forklares ved, at den nedre horisonts insekter er blæst ud over havet noget tidligere på året end insekterne fra den øvre horisont.

Sammensætningen af insekter i Moléret er meget forskellig fra den forholdsvis velkendte fauna i det omtrent jævnaldrende baltiske rav og fortjener en grundig videnskabelig behandling.

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