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THE MESOZOIC MAYFLIES (EPHEMEROPTERA) WITH SPECIAL REFERENCE TO THEIR ECOLOGY

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Abstract. Possibly the Late Carboniferous and Early Permian mayfly nymphs were primarily either non aquatic or exclusively lotic. Jurassic and Early Cretaceous mayfly assemblages are all lacustrine, poor in number of species but often abundant in number /abundance or predominance of presumably highly oxyphilous forms/. Most of mayflies have more or less siphlonuroid-like nymphs with large gills on the sides of abdomen, classified to some extinct /Hexagenitidae, Epeoromimidae/ as well as to some living families /Siphlonuridae, Leptophlebiidae/. Typical Jurassic and Early Cretaceous lakes hardly fit the common lake classification and represent extinct ecosystem types. At the beginning of Late Cretaceous aquatic insects were probably exterminated by the eutrophication of standing waters caused by angiosperm leaf litter.

Paleontology, aquatic habitats, coenoses, abundance, Siberia

A survey of all fossil mayflies with the discussion of the main trends of their evolution has recently been given by O. A. Tshernova (Tshernova 1980), so we concentrate on the ecological evolution of the order, the more so that the subject has not so far been explored on the basis of paleontological data.

Mayflies are known from Late Carboniferous, but only a short section of their history is well reflected in the fossil record, namely Jurassic and Early Cretaceous. Carboniferous mayflies are known from sole imprint of the imago of Triplosoba pulchella (Brongniart, 1893). Nothing definite can be said on its ecology. The nymphs are supposed to be primarily non aquatic.

Permian fossils are more numerous. Particularly we know a number of remnants of nymphs from the Lower Permian of Cze-

choslovakia and the USA. At that time they already possessed aquatic life adaptations and probably were lacustrine; at least they were buried in lake deposits. The Permian nymphs belong to the following three families: Protereismatidae, Jarmilidae and Kukalovidae (Kukalová 1968; Hubbard and Kukalova-Peck 1980).

The early appearance of water mayfly nymphs allows to suppose that the mayflies have possibly been the first among the insects to turn to aquatic mode of life.

Morphologically the Palaeozoic mayflies differ greatly from the younger ones; they are separated into the suborder Protereismatoidea. The Palaeozoic mayflies are characterized by homonomous wings and not fully reduced mouthparts of imago; the nymphs have five-joined tarsi and nine pairs of gills. All the Mesozoic mayflies have the hind wings shorter than the fore ones, the number of nymphal gills is reduced to seven.

Contrary to the Palaeozoic ones, where imagoes always prevail over the larvae, in the Triassic deposits we find localities with mass of aquatic insect larvae. However, despite the Triassic localities with fossil evidence of insects are known in a great number and are evenly distributed on all the continents, the mayfly remnants are very rare. The only family Mesoplectopteridae is known from the Triassic, the representatives of which have been found in the Permian as well.

The post-Triassic mayfly fossils are numerous, especially those of immature stages. Almost all known nymphs have surely been lake inhabitants. It is because they were buried in lake deposits, and a mass burial of nymphs of a few species indicated that they lived in that lakes. The rheophilous nymphs can be transported into lakes and buried there only by chance and their remnants can be found only rarely among true lacustrine nymphs (Sinitchenkova 1976). For instance, thousands of limnic mayfly nymphs should be collected before four remains of definitively rheophilic nymphs can be found: two in the Upper Jurassic of Transbaicalia (Tshernova 1977), one in the Upper Oligocene of the Sikhote-Alin (McCafferty and Sinitchenkova 1983) and one in Neogene of West Siberia (Tshernova 1962). Each of them belongs to a different family: Behningiidae, Palingeniidae, Ephemeridae and Heptageniidae respectively. From the paleontological point of view all the remaining rheophilous species are known only as imagoes embedded into fossil resin (Demoulin 1956, 1968; Tshernova 1971). It is natural because the resin (e.g. amber) could be transported by water of streams before its concentration in the marine coastal deposits.

Known Jurassic mayflies belong to approximately twenty species, fourteen genera and nine families. Most of them are found in Asia. Outside Asia only imago remnants of Mesephemeridae and Hexagenitidae were found at the famous Upper Jurassic locality Solnhofen. Mayflies, found only if a great number of fossil insects are collected, are quite uncommon at this locality. After reconstruction, the locality in Solnhofen repre-

sents a sea-lagoon where the winged mayflies brought by wind from the neighbouring land were buried. Europe was not a continent in the Jurassic, but represented rather an archipelago. The scarcity of mayfly fauna in Europe can be compared with the impoverishment of recent islands biocoenoses, due to a relatively very low settling ability and dispersal of mayflies. On the continents, which in Mesozoic represented big lithosphere plates with large land areas, the mayfly remains are found or should be found in a great number.

The Jurassic mayflies occur in Siberia, Mongolia and China in Asia.

Several types of the inhabited by mayflies lakes are reconstructed in Siberia. These data have not been published yet. All the types of Jurassic lakes in Siberia are, first of all, characterized by oxyphilous insect fauna, reduced trophication and low mineralisation of water. The deposits of these lakes contain a great number of remains of such oxyphilous insects as stoneflies, while the filtrators are practically absent.

Different types of Jurassic lakes in Siberia are bound up with different stages of the Siberian landscape formation. To the west of Baical mayflies are found in the Lower or Middle Jurassic deposits formed in small shallow flood-lands which have arisen during floods of rivers and lakes in well developed valleys. At some localities Epeoromimus kazlauskasi Tshern. (family Epeoromimidae) dominates among the mayflies at other localities Mesobaetis sibirica Brauer, Redtenbacher and Ganglbauer (Siphlonuridae) and Mesoneta antiqua Br., Rdtb., and Ganglb. (Leptophlebiidae) are dominating. In similar reservoirs in West Mongolia the mayfly nymphs of the family Hexagenitidae referred to a new genus Siberiogenites (S. rotundatus) are found together with Mesobaetis sibirica as well.

In Transbaicalia a high tectonic activity and intensive volcanism are recorded during the Jurassic. Insectiferous deposits are considered to be of the same age or younger: some of them are dated by the end of the Early or Middle Jurassic, others by the Late Jurassic. The deposits formed in lakes in most cases represented mill-ponds in mountainous territory. The climate was apparently milder than that west of the Baical. Small lakes in narrow river valleys was formed due to damming of the rivers by lava-streams. The banks of lakes were rocky with poor vegetation. The stonefly fauna evidently differs from that of the above mentioned lakes; these lakes have neither common species, nor even any common genus. The changes in mayfly fauna have not been so radical. In the Lower or Middle Jurassic deposits Mesobaetis sibirica (dominating), Mesoneta antiqua and Siberiogenites angustatus (the second species of this genus) are also found but they are extremely rare.

The Late Jurassic mayfly fauna of Transbaicalia had greater differences as there were no species in common. Stackelbergisca sibirica Tshern. and yet undescribed species of Mesoneta dominated there. The burrowing nymphs of the Palingeniidae - Mesogenesia petersae Tshern. and the nectonic nymph of the Behningiidae - Archaebehningia edmundsi Tshern. are found in

these deposits (Tshernova 1977). There is no doubt that the mayflies of these groups arose much earlier but because of their special mode of life they seldom penetrated into taphocoenoses. In that period a few new Siphlonuridae have appeared (descriptions in print).

Early Cretaceous mayflies are more widespread than the Jurassic ones. At present they are known from Europe and North Africa (Hexameropsis selini Tshern. et Sinitch. and H. africana Sinitch.), from Asia (except South-East Asia) where Ephemeropsis trisetalis Eichw., widespread in Siberia, Mongolia, North China and Corea predominates (Sinitchenkova 1975, Tshernova 1961, Tshernova and Sinitchenkova 1974). There is a record on mayflies from Australia (Riek 1970), and they are also found in Brazil. Judging from the materials, kindly sent to me by Dr. Maria Volcano from Saõ Paulo, Hexagenitidae represented also a dominating group in Brazil. This family probably represented by Hexameropsis in Brazil and in West Mongolia (undescribed material), too. Taking into account that in Early Cretaceous Hexagenitidae dominated all over the world one can almost faultlessly predict their findings in India and in central parts of Africa from where the mayfly remains are unknown so far.

Asian Early Cretaceous limnic assemblages are poor in benthos, characterized by oxyphily, abundance of nectonic forms and absence of filtrators (Ponomarenko and Kalugina 1980). The nectonic adaptations (immovable articulation of tarsus joints furnished with a thick fringe of swimming hairs) are acquired even by the dragonfly nymphs (the only known case within this order). One may suppose that the hexagenitid nymphs spread widely in the Early Cretaceous as they had managed to adapt to the nectonic mode of life better than the others. Considerably strengthened gills typical for the family were probably their leading adaptation to the nectonic habits.

The similarity of the morpho-ecological types of limnetic mayfly nymphs in the Jurassic and the Early Cretaceous attracts an attention. Such type seems to have no recent equvivalent. The nymphs had siphlonuroid-like appearance with more or less large gills always outstretched when preserved. Such gills disposition in fossils probably reflects that in lifetime. It was supposed earlier that the Mesozoic mayfly nymphs had moved among aquatic vegetation. However, the recent mayflies living among aquatic vegetation have either large gills which lie on the dorsal surface of abdomen (as in Siphlonurus) or narrow divided gills lying along the abdomen (as in Heptagenia). The recent mayflies with the gills protruding to the sides as a rule inhabit some stony ground but their gills are not so large (as in Ameletus).

Possibly the Mesozoic mayflies lived in the reservoirs with stagnant water (unlike Ameletus) not overgrown with the aquatic vegetation (unlike Siphlonurus and Heptagenia). Such reconstruction of the mayfly mode of life agrees better with

geological and paleobotanical data indicating the absence of rich flora of submerged plants in the Mesozoic. Only one lacustrine Mesozoic mayfly Proameletus caudatus Sinitch. had small gills (as in Ameletus)(Sinitchenkova 1976). The age of the deposits with Proameletus is disputable; some specialists date them by the end of the Early Cretaceous, the other ones by the Upper Jurassic.

During the Upper Cretaceous and the Paleogene limnophilous insect fauna disappeared from orictocoenoses. Limnetic biocoenoses evidently underwent drastic change in the middle of Cretaceous (Kalugina and Zherichin 1975; Zherichin 1978). The agens which caused this change was probably distribution of the angiosperm vegetation resulting in change of soil and freshwater chemistry (Kalugina 1974, 1980). From that time the findings of mayflies especially of the nymphs become extremely rare.

Thus we can see that Mesozoic stage of mayfly evolution differs sharply from the Paleozoic and Caenozoic ones. In different Mesozoic periods the development of mayfly faunas was also different. In the Triassic the formation of the Mesozoic assemblages of aquatic insects may have begun; the Jurassic and Early Cretaceous were the time of flourishing of lacustrine mayflies stopped abruptly at the beginning of the Late Cretaceous. The composition of the fauna changed in time and space during the Mesozoic but the general ecological type remained unaltered. The taxonomic diversity of the Mesozoic mayflies was not pronounced but their role in the aquatic biocoenoses was probably considerable because they were abundant in number. Almost certainly their role in limnetic biocoenoses was much more important than now - at least because fossil mayfly nymphs are extremely rare even in young deposits including the Late Neogene.

REFERENCES

Demoulin, G. 1956. Electrogenia dewalschei n.gen. n.sp., Ephéméroptère fossile de l'ambre. Bull. Ann. Soc. R. Ent. Belg., 92: 95 - 100.

Demoulin, G. 1968. Deuxième contribution à la connaissance des Ephéméroptères de l'ambre oligocène de la Baltique. Dtsch. ent. Z., 15: 233 - 276.

Hubbard, M.D. and Kukalova-Peck, J. 1980. Permian mayfly nymphs: new taxa and systematic characters. In: Flannagan, J.F. and Marshall, K.E. (eds.): Advances in Ephemeroptera biology, p. 19 - 31. Plenum, N. York, London.

Kalugina, N.S. 1974. Evtrofirovanie kak odna iz vozmozhnykh prichin perestroyki vodnykh biocenozov v konce mezozoya. In: Antropogennoe evtrofirovanie vodoemov. Tez. Dokl. I. Vses. simpoziuma po antropolog. evtrof. vodoemov. Chernogolovka, 1974, p. 137 - 139.

Kalugina, N.S. 1980. Nasekomye v vodnykh ekosistemakh proshlogo. In: Istoricheskoye razvitie klassa nasekomykh. Tr. Paleontol. Inst. AN SSSR, 175, Nauka, Moskva, p. 224 - 240.

Kalugina, N.S. and Zherichin, V.V. 1975. Izmenenie limnofauny nasekomykh v mezozoe i kaynozoe i ikh ekologicheskaya interpretaciya. Tez. Dokl. IV. Vses. simpoz. po istorii ozer. I, p. 55 - 61.

Kukalová, J. 1968. Permian mayfly nymphs. Psyche, 75: 310 - 327.

McCafferty, W.P. and Sinitchenkova, N.D. 1983. Litobrancha from the Oligocene in Eastern Asia (Ephemeroptera: Ephemeridae). Ann. ent. Soc. Am., 76: 205 - 208.

Ponomarenko, A.G. and Kalugina, N.S. 1980. Obshtchaya charakteristika nasekomykh mestonakhozhdeniya Manlay. In: Rannemelovoe ozero Manlay. Tr. sovm. Sov.-Mong. Paleontol. exp., 13: 68 - 81.

Riek, E.F. 1970. Lower Cretaceous Fleas. Nature, 227: 746 - 747.

Sinitchenkova, N.D. 1975. Litchinki podenok semeystva Hexagenitidae (Insecta, Ephemeroptera). Paleontol. zh., 1: 82 - 86.

Sinitchenkova, N.D. 1976. Novye rannemelovye podenki (Insecta, Ephemeroptera) iz Vostotchnovo Zabaykalya. Paleontol. zh., 2: 85 - 93.

Tshernova, O.A. 1961. O sistematitcheskom polozhenii i geologitcheskom vozraste podenok roda Ephemeropsis Eichwald (Ephemeroptera, Hexagenitidae). Ent. obozr., 40: 858 - 869.

Tshernova, O.A. 1962. Litchinki podenok iz neogena Zapadnoy Sibiri (Ephemeroptera, Heptageniidae). Zool. zh., 41: 943 - 945.

Tshernova, O.A. 1971. Podenki iz iskopaemoy smoly melovykh otlozheniy polyarnoy Sibiri (Ephemeroptera, Leptophlebiidae). Ent. obozr., 50: 612 - 618.

Tshernova, O.A. 1977. Svoeobraznye novye litchinki podenok (Ephemeroptera: Palingeniidae, Behningiidae) iz yury Zabaykalya. Paleontol. zh., 2: 91 - 97.

Tshernova, O.A. 1980. Otryad Ephemerida. Podenki. In. Istoricheskoye razvitie klassa nasekomykh. Tr. Paleontol. Inst. AN SSSR, 175, Nauka, Moskva, p. 31 - 36.

Tshernova, O.A. and Sinitchenkova, N.D. 1974. Noviy rod i vid iskopaemykh podenok semeystva Hexagenitidae (Ephemeroptera) s yuga evropeyskoy tchasti SSSR i ikh svyaz s sovremennymi podenkami. Ent. obozr., 53: 130 - 136.

Zherichin, V.V. 1978. Razvitie i smena melovykh i kaynozoyskikh faunistitcheskich kompleksov (trakheynye i khelicerovye). Tr. Paleontol. Inst. AN SSSR, 165, Nauka, Moskva, 197 pp.