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Main ecological events in aquatic insects history

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Abstract. In the Carboniferous no one undoubtedly aquatic insect remain is found. Mayflies and stoneflies were the oldest aquatic insects found in the Early Permian. Permian was the time when the aquatic insects became diverse and probably colonized different types of waters. Only one mayfly is found in the Early Triassic. The Middle and Late Triassic aquatic insect assemblages are characterized by combination of Paleozoic and Mesozoic elements. Diverse and widespread lacustrine insects are typical for the Jurassic. Recent families of aquatic insects appeared in the Early Cretaceous. The Late Cretaceous assemblages are considerably impoverished. The Cenozoic is the time of recolonization of lacustrine habitats.

Key words: aquatic insects, history, Carboniferous, Permian, Triassic, Jurassic, Cretaceous, Cenozoic, palaeoentomology.

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I. INTRODUCTION

Aquatic insects play most important role in modern fresh water ecosystems. Different, phylogenetically unrelated taxa with different types of development (both Holo- and Hemimetabola) are associated with aquatic environments. They differ in feeding habits as well, including detritivores, herbivores and predators.

It is necessary to stress also the differences in the breathing mechanisms. Immature stages of the mayflies, stoneflies, megalopterans, caddisflies, as well as some dipterans and beetles breathe with dissolved oxygen, while adults and larvae of most beetles and bugs and immatures of some dipterans breathe with atmosphere air and hence do not depend on the oxygen concentration in water. It is plausible to assume that they had different patterns of colonization of aquatic environments because of very different required adaptations.

The statement that the insects are secondarily aquatic animals, which had evolved from terrestrial ancestors seems to be out of any serious doubt now. It is demonstrated that the wingless insects existed in terrestrial habitats as early as in the Devonian. The oldest finds of winged insects come from the Early Carboniferous (Namurian A) while the earliest undoubtedly aquatic insects appear only in the Permian.

For recognizing aquatic insects among the fossils WOOTTON (1988) has proposed three criteria. The main evidence of the aquatic mode of life he considered the presence of special adaptations for aquatic life, such as swimming legs, gills and fringed caudal filaments. Less reliable criteria are based on phylogenetic affinities of fossils with present-day aquatic taxa.

WOOTTON considers relation of a given fossil to a group originated from an aquatic ancestor to be more reliable indication than when it belongs to a group with an uncertain way of life. The WOOTTON's criteria should be supplemented by the taphonomic ones, first of all by repeated fossil finds of immature stages for which the probability of burial if they were terrestrial is low. It is the most unreliable criterion. For instance, the aquatic mode of life has been suggested for some Permian grylloblattids when basing on their frequent finds. Recent investigation of their body structure demonstrated characteristic terrestrial features, so their aquatic life has been rejected completely (STOROZHENKO 1998). It is necessary to take in consideration also the presence of ichnofossils in the case when their classification to a definite group is well argued.

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II. CARBONIFEROUS TO PERMIAN

No Carboniferous insects demonstrating any obvious adaptations to aquatic mode of life are known. As far as the taxonomic criteria are concerned, the Carboniferous mayfly-like Syntonopterida and dragonflies of the suborder Meganeurina could be proposed. For the Carboniferous nymph *Bojophlebia* (KUKALOVA-PECK 1985) an aquatic habit is doubtful. KLUGE (1996) considers it to be a terrestrial insect related to Tysanura rather than a mayfly-like nymph.

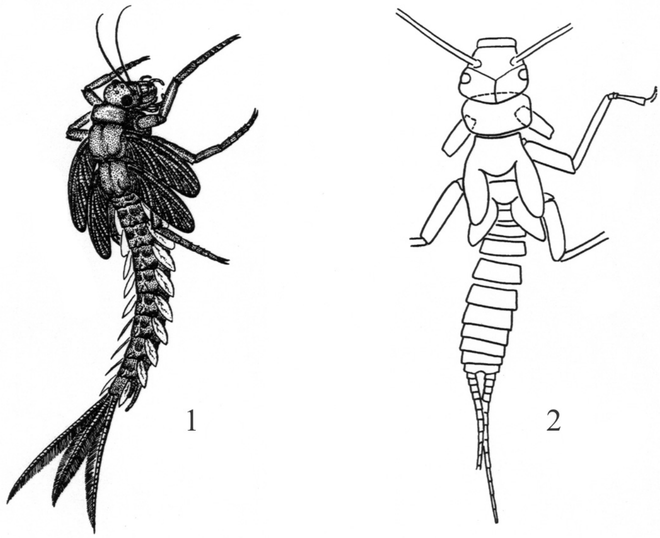
Adult Meganeurina are abundant in the Carboniferous but complete absence of their nymphs in the fossil record made PRITYKINA (1980) to suggest terrestrial habits for the Paleozoic odonatans.

An aquatic or semiaquatic way of life seems to be probable for Dasyleptidae – a peculiar extinct group of the order Machilida occasionally common both in the Carboniferous and Permian. No modern bristletails are aquatic, and dasyleptids demonstrate no special morphological features for living inhabiting in water; however, their common presence in the fossil state is unique among the apterygotans. The ichnofossils from the Late Carboniferous estuary deposits of Kansas were supposedly attributed to dasyleptids (MÁGNANO et al. 1997). If this attribution is correct, Dasyleptidae could prove to be the only Carboniferous insect family whose aquatic mode of life is quite probable. When taking in consideration that it belongs to the order that is exclusively terrestrial now, there is no continuity between the Carboniferous and post-Paleozoic aquatic insect faunas.

In any case the insects did not play any essential role in the Carboniferous fresh water ecosystems. This fact fits well the general opinion about pronounced differences between those ecosystems and the modern ones; however, the available data on insects do not allow to specify those differences in a more precise way.

The first unequivocally aquatic immatures of winged insects enter fossil record in the Permian. They include the mayfly and stonefly nymphs. However, their finds still remain rare in comparison with the fossil adults of the same groups. The Early Permian mayfly nymphs (Fig. 1) are found in Oklahoma, USA, in the Czech Republic, Central Europe (HUBBARD & KUKALOVA-PECK 1980), and in the Urals in the famous locality Tshekarda (TSHERNOVA 1965). They represent two extinct families, Protereismatidae in America and Central Europe, and Misthodotidae in Russia. Their laminated abdominal gills (or tergaliae) and fringed caudal filaments indicate an aquatic mode of life.

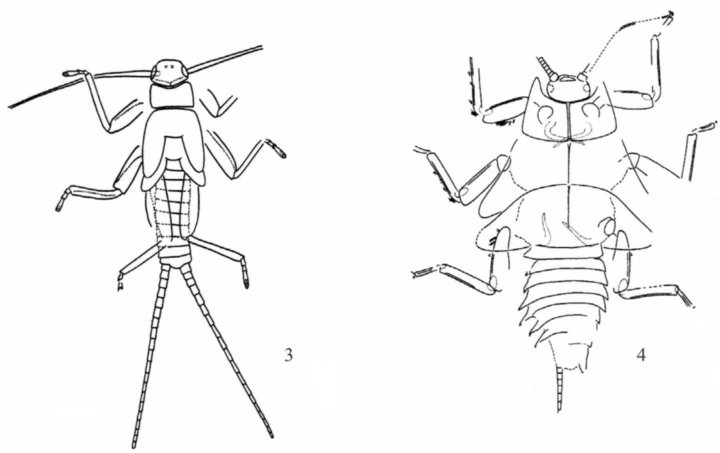
Several stonefly nymphs of the family Tshekardoperlidae (Fig. 2) are collected in Tshekarda together with the misthodotid mayflies (SINITSHENKOVA 1987). The tshekardoperlid adults still remain undiscovered. Numerous adult stoneflies found in the same locality are assigned to other families - Palaeonemouridae and Perlopseidae (SINITSHENKOVA 1987). Tshekardoperlid nymphs were probably carnivorous. They had no gills, and their aquatic mode of life can be postulated only on the base of their general similarity with modern perloid stoneflies. However, in Tshekarda an-



Figs 1-2. The Early Permian aquatic insects. 1 – mayfly *Kukalova americana* DEMOULIN, Protereismatidae, Oklahoma, USA (after KUKALOVA-PECK 1968); 2 – stonefly *Sylvoperlodes zhiltzovae* SINITSH., Tshekardoperlidae, Urals, Russia (after SINITSHENKOVA 1987).

other stonefly nymph is found, which shows quite obvious adaptations for inhabiting fast running water (the rhithral zone). This is *Barathronympha victima* (Fig. 3) having the streamlined body, the cerci moved apart widely, the flattened and widened femora and numerous short hairs on the tarsi lacking the claws (SINITSHENKOVA 1987). Those characters are unique among the stoneflies, so that the nymph resembles superficially a heptageniid mayfly rather than a stonefly.

One more remarkable nymph of uncertain systematic position is described from Tshekarda. *Sylvonympha tshekardensis* possesses the thoracic gills similar to the coxal gills of stoneflies (Fig. 4) but cannot be assigned to this order and seems to represent an extinct lineage (NOVOKSHONOV & PAN'KOV 1999).



Figs 3-4. The Early Permian aquatic insects of Urals, Russia. 3 – stonefly *Barathronympha victima* SINITSH., Nemouromorpha inc. sed., (after SINITSHENKOVA 1987); 4 – *Sylvoperlodes tshekardensis* NOVOKSH. et PAN'KOV, Perlidea, (after NOVOKSHONOV & PAN'KOV 1999).

In Tshekarda insects occur in deltaic deposits of a large river. The mayflies and tshekardoperlid stoneflies could inhabit this river, while *Barathronympha* dwelled most probably in a small rapid stream.

The caddisflies appear in the Early Permian as well but they are represented exclusively by fossils of adults, and the biology of their larvae is a matter of speculations. If they had inhabited some protected microhabitats in running waters like many modern annulipalpian larvae do, they had little if any chance to be preserved as fossils. In younger deposits, including the Cenozoic, the lotic caddisflies are represented by adults and occasionally by the integripalpian larval cases but the annulipalpian larval fossils are totally absent.

Dasyleptids still survived in the Early Permian; they are rather common in some areas (e.g., in Kansas, USA) but never occur together with other aquatic insects. The most striking feature of the Early Permian aquatic insects is that they never occur in lacustrine sediments, unlike the younger deposits. The Early Permian finds seem to be restricted to deltaic and estuarine paleoenvironments. The diversity of insects is usually very low, except the Tshekarda assemblage.

Further enrichment of the aquatic entomofauna is documented in the Late Permian (Fig. 5). The mayflies are represented exclusively by winged stages. Some of them are related to the Early Permian Misthodotidae (Kinzelbach & Lutz 1984), while others resemble modern ephemeroids and may belong to this lineage (Martynov 1931). In the both cases nymphal aquatic mode of life is quite probable, supposedly in large rivers.

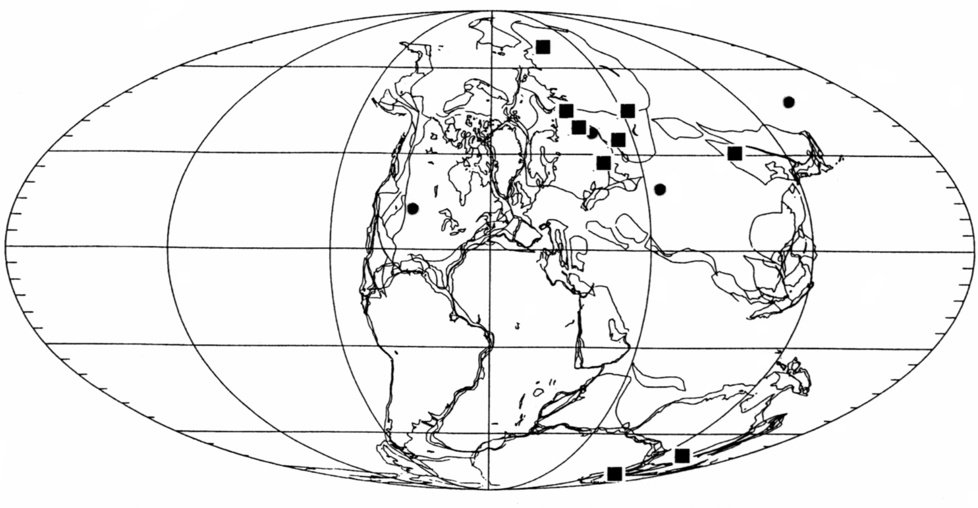


Fig. 5. The Permian sites with aquatic stages of insects. ● – Early Permian; ■ – Late Permian.

Stoneflies occur in the Late Permian more often than in the Early Permian, but the finds of adults still dominate. However, in the lacustrine deposits of West Siberia and Kazakhstan the stonefly nymph remains are sometimes quite common. This fact permitted to propose their invasion to standing waters. It is clear that in the Late Permian the stoneflies were diverse, widely distributed and inhabited, probably, different types of water bodies (Sinitshenkova 1987).

Megalopterans are the only holometabolan insect order represented in the Late Permian by both adults and larvae (Fig. 6) with characteristic abdominal gills (Sharov 1953; Ponomarenko 1976, 2000).

Fig. 6. The Late Permian dobsonfly *Permosialis* sp., Orenburg region, Russia (after SHAROV 1953).

The schizophoroid beetles appear in the Late Permian and at once in many localities of Europe, Asia, Australia, South America and South Africa. The presence on their elytrae of a special closing device (the so-called "schiza") resembling that of living aquatic beetles permitted PONOMARENKO (1969) to suggest aquatic life for them. If so, schizophoroids are the oldest pterygotans with aquatic adults. Their larvae are unknown.

Like in the Early Permian, the caddisflies are not rare but represented only by adults. The youngest Dasyleptidae are known from the Late Permian of West Siberia. They are restricted to the only locality Kaltan where stonefly nymphs occur as well in fine-grained sediments (RASNITSYN 2000).

Thus, in the Permian the aquatic insects become diverse and probably colonized gradually different types of waters, both running and standing. The occurrence of the Carboniferous and Early Permian finds of aquatic stages and ichnofossils in estuarine and deltaic deposits seems to confirm the statement of WOOTTON (1972) that the insects inhabited at first the running waters. However, in my opinion this assumption seems rather disputable. Life in running waters suggests considerable level of specialization including diverse morphological adaptations (e.g., to fixing on the substrate) as well as specialized behavior with upstream flights of adults to compensate the drift of immature stages. Hence true lotic insects should be rather advanced in comparison with early water colonizers.

In my view, periodically flooded habitats are the most probable biotopes of ancestral aquatic insects; this scenario was postulated earlier by PONOMARENKO (1996). Many terrestrial insects devoid of evident special adaptations can survive temporarily submersion. For them the colonization of aquatic environments should be rather simple and gradual. This way of colonization may be called a passive one. If such a passive colonization took place, then it is not surprising that the oldest aquatic insects occur just in deltaic and estuary paleoenvironments where temporary flooding must have been a common event. Appearance of morphologically highly specialized rheophilous nymphs in the Early Permian indicates an early expansion from near-shore habitats to the riverbed. Possibly, an important factor of such specialization was the protection of long-developing immatures from the terrestrial and air predators. It is noteworthy that flying adults of the most ancient aquatic groups – e.g., the stoneflies, megalopterans and especially mayflies – became short living.

The WOOTTON's idea that the earliest aquatic insects were carnivorous (WOOTTON 1972) gives rise to doubt. In particular, the Carboniferous dasyleptids were probably detritivorous. In the Permian the groups with different feeding types are known, including detritivores and possibly grazing algophages (mayflies, some stoneflies, possibly schizophoroid beetles) as well as predators (some stoneflies, megalopterans).

III. TRIASSIC

In the Early Triassic few insect finds are known, and only one mayfly adult has been recently found in Siberia. Hence all our knowledge refers to the Middle and Late Triassic (Fig. 7). The dasyleptids are absent in the Triassic but all insect orders which appeared in the Permian not only survived but also even become more numerous and wider distributed.

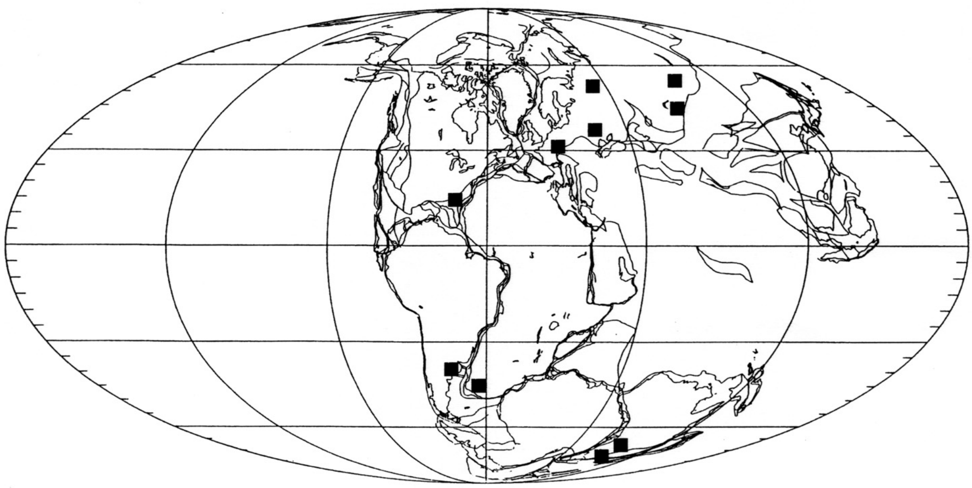


Fig. 7. The Triassic sites with aquatic stages of insects.

Several orders are adding to the aquatic insect list in the Triassic, including the aquatic bugs and dipterans as well as the most ancient undoubtedly aquatic odonatan nymphs in the Upper Triassic of Australia (ROZEFELDS 1985).

Among the Triassic mayflies there are both the Permian survivors (Misthodotidae) and typically Mesozoic groups (*Mesoneta* BRAUER, REDTENBACHER, GANGLBAUER, 1889; *Mesobaetis* BRAUER, REDTENBACHER, GANGLBAUER, 1889) (SINITSHENKOVA 2000). The largest and richest Triassic mayfly assemblage is discovered in the Grés-à-Voltzia deposits of the Vosges, France (MARCHAL-PAPIER 1998). At present seven species are preliminary recognized as the nymphs, all but one previously undescribed. The most interesting are two species with unusually strong cuticle suggesting that they possibly could survive in wet substrates at the shore zone. The oldest burrowing mayfly nymphs are found as well.

Triassic stoneflies are widespread but represented mainly by adults. The nymphs are rather uncommon; some Late Triassic nymphs are assigned to several genera common in the Jurassic (SINITSHENKOVA 1987).

The aquatic bugs are represented by rare Triassocoridae and supposed Naucoridae in the Middle and Late Triassic of Ukraine, Central Asia and Australia (POPOV 1980; POPOV, pers. comm.). The oldest numerically rich aquatic bug assemblage is discovered in the Uppermost Triassic of North America (the Caw Branch Formation) (OLSEN et al. 1978; FRASER et al. 1996).

The undescribed megalopteran larvae with well-developed abdominal gills are found in France and Ukraine (KALUGINA 1980). The schizophoroid beetles are common and diverse in the Triassic over the World, and the oldest hydradephagan beetles are appearing at that time (PONOMARENKO 1969; ARNOLDI et al. 1977). The caddisflies are represented exclusively by adults.

Appearance of aquatic dipterans was likely the most important Triassic novelty in the aquatic insects fauna if the importance of the order in all younger aquatic ecosystems is taken into account. Dipteran larvae and pupae are found in Vosges Mts but not studied yet (MARCHAL-PAPIER 1998).

In spite of the relative scarcity of data, it is possible to say with certainty that the Triassic was the time of considerable radiation of aquatic insects, both lotic and lentic. This radiation suggests that the hydrological and hydrochemical regime of standing water bodies became more stable in comparison with the Paleozoic. In particular, in the Late Triassic the oldest lotic assemblages closely resembling some widespread Jurassic types (e.g., with abundant aquatic bugs and with the mesoleuctrid stonefly nymphs) are discovered.

IV. JURASSIC

The Jurassic insects are studied much better but mainly in North Asia. In Europe the Jurassic insects are found principally in allochthonous oryctocenosis in marine deposits. In the North America and Gondwanaland only few localities are known. All aquatic orders known in the Triassic are present in the Jurassic, and are considerably more diverse.

The mayflies, stoneflies and odonatans belong mostly to extinct families (Fig. 8-10). The diversity of the former two orders is higher in more temperate interior regions of Asia while diversity of the odonatans culminates likely in warmer central Asia and Europe (TSHERNOVA 1967, 1969, 1977; SINITSHENKOVA 1987).

The aquatic bugs are diverse and widely distributed. The aquatic beetles are common and their diversity is also rather high; the role of hydradephagan beetles is increasing while the schizophoroids decline gradually. The hydradephagan larvae are not rare and include both benthic and actively swimming nectic forms (PONOMARENKO 1995).

In the Early Jurassic the recent mecopteran family Nannochoristidae appears in palaeontological record for the first time. This is the only living aquatic group within the order. The nannochoristid wings are not uncommon but the larval fossils are extremely rare (NOVOKSHONOV 1997). Their rarity suggests that they probably dwelled in small streams like their modern relatives do. Nannochoristid larvae were active predators inhabiting running waters.

The Jurassic caddisflies are represented mainly by the primitive and probably unnatural annulipalpian family Necrotauliidae but there are other families as well including some primitive integripalpians. In the Upper Jurassic of Siberia, Mongolia and North America the caddisfly larval cases appear in paleontological record for the first time (SUKATSHEVA 1985). Since that time they became a basic component of lacustrine benthos. It is interesting to note that the case-building larvae are algal-feeders and detritivores, with very few predators.

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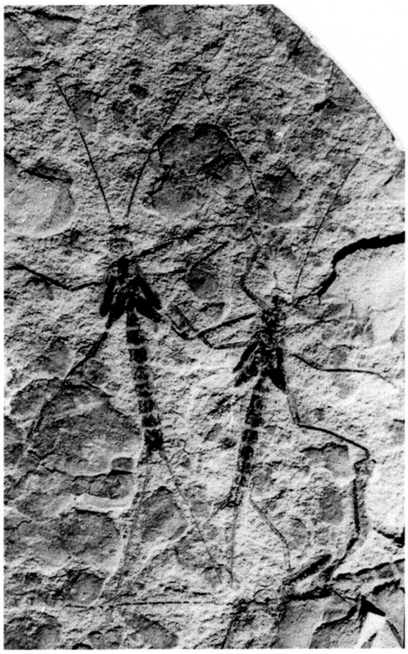

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Figs 8-9. Stoneflies from Early or Middle Jurassic of Siberia, Russia (after SINITSHENKOVA 1987). 8 – *Platyperla platypoda* BRAUER, REDTENBACHER, GANGLBAUER 1889, Platyperlidae; 9 – *Mesoleuctra tibialis* SINITSH. Mesoleuctridae.

10

Fig. 10. Mayfly *Epeoromimus kazlauskasi* TSHERNOVA, Epeoromimidae, Early or Middle Jurassic of Siberia, Russia (after TSHERNOVA 1969).

Since the Early Jurassic the nematoceran dipterans (in particular Chaoboridae and Chironomidae) became extremely common in the lacustrine deposits (KALUGINA 1980).

Thus, in the Jurassic the taxonomic and ecological diversity of aquatic insects, especially in lakes, are considerably higher in comparison with the Triassic. Some Jurassic freshwater ecosystems were likely basically similar to recent ones, e.g. the ecosystems of oligotrophic cold-water montane lakes and streams. On the other hand, we failed to find any modern analogs for some other Jurassic ecosystems, e.g. for the small oxbow lakes of North Asia (SINICHENKOVA & ZHERIKHIN 1996).

V. CRETACEOUS

The Cretaceous aquatic insects are well represented in the paleontological record both in the northern continents and in Gondwanaland. The Early Cretaceous aquatic insect assemblages are diverse and taxonomically rich. They often include the families and even genera common in the Jurassic, and that is why the age of some deposits is disputable. On the contrary, the Late Cretaceous assemblages are extremely impoverished and remarkably uniform. It should be stressed that since the Cretaceous the insects occur in the fossil resins (ambers) that provides a valuable source of information about the running water fauna.

Among the mayflies the family Hexagenitidae is often most abundant , both in the north hemisphere (Asia) (TSHERNOVA 1980) and in the south hemisphere (Brazil) (MCCAFFERTY 1990). Different families dominate some Asiatic assemblages and the Koonwarra fauna in Australia (JELL & DUNCAN 1986). The burrowing mayfly nymphs are abundant in some sites. No lentic mayflies are known from the Late Cretaceous while the lotic fauna was rather diverse as indicated by resin inclusions from Asia and North America.

In comparison with the Jurassic the role of heterophlebioid and isophlebioid odonatans (the so-called Mesozoic anisozygopterans which, however, had a little in common with the living Epiophlebiidae) decreases considerably, and the radiation of anisopteran dragonflies of the suborder Libellulina is observed. The dragonflies are represented mostly by wings. Their nymphs may occur in mass in lacustrine deposits but are always much less diverse than adults, which suggests that the majority of species developed outside large lakes (PRITYKINA 1980; JELL & DUNCAN 1986; BECHLY 1998). The species diversity of the Early Cretaceous dragonflies obviously decreased from the warm regions in favor of the more temperate ones, just like it was in the Jurassic. The true zygopteran damselflies are extremely rare. In the Late Cretaceous the odonatan fossils are represented nearly exclusively by adults.

The stoneflies become uncommon and only rarely occur in considerable numbers in Cretaceous deposits. However, their total diversity seems to increase in the Early Cretaceous because the main Jurassic families still occur and some Recent ones enter the fossil record for the first time. All ecological types of nymphs which existed in the Jurassic are known from the Early Cretaceous. Till now no stonefly remain from the Late Cretaceous is found (SINITSHENKOVA 1987).

Aquatic bugs are common, diverse and widespread in the Early Cretaceous, especially the corixids and notonectids. Unlike many other aquatic insects, bugs occur in Late Cretaceous lacustrine deposits as well although the frequency of finds is rather low (POPOV 1980; JELL & DUNCAN 1986).

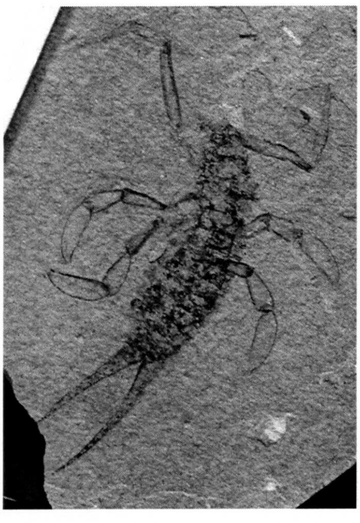
The dobsonflies are represented mainly by the corydalid larvae of the genus *Cretachaulus* PONOMARENKO, 1976, common in the lacustrine Early Cretaceous deposits of Transbaikalia.

The Early Cretaceous aquatic beetles are represented mainly by the same families as in the Jurassic, and the set of ecological groups is similar as well. They occur in different deposits, sometimes where no other aquatic insects are found. In the Late Cretaceous some most peculiar Mesozoic taxa had disappeared completely (e.g., coptoclavids). The appearing of aquatic leaf beetles of the subfamily Donaciinae in the Latest Cretaceous is noteworthy.

The caddisflies evolved rapidly in the Early Cretaceous. Lacustrine assemblages are dominated by several integripalpian families, first of all by extinct Vitimotauliidae, although some necrotauliids still survive as well. Fossil larval cases show rapid behavioral evolution over the Early Cretaceous. At the very end of the Early Cretaceous the diversity of caddis cases in lacustrine assemblages fell drastically suggesting an extinction of the majority of lentic taxa. In the Late Cretaceous the lacustrine assemblages are extremely poor in species (usually one or two in each). On the other hand, resin inclusions document radiation of modern families, both annulipalpian and integripalpian, probably mainly in running water environments.

The dominating aquatic dipteran families in the Early Cretaceous are the same as in the Jurassic. The first appearance of aquatic brachyceran fly larvae is worth of mentioning. On the contrary, in the Late Cretaceous few dipteran fossils occur in lacustrine deposits, in a strong contrast with diverse running water fauna represented in fossil resins. In particular, no chaoborids occur in lacustrine deposits.

In the Jurassic and especially in the Early Cretaceous lakes the diversity of aquatic insects possessing special adaptations to swimming attracts attention. Some of them are rather unusual, like the larvae of coptoclavid beetles (Fig. 11), and especially the nymphs of hemeroscopid dragonflies (Fig. 12). The latter group is unique among the odonatans in its swimming adaptations. Possibly the mayfly nymphs of the family Hexagenitidae (Fig. 13) could be referred to the nectobenthic swimming fauna too. They have wide gills (tergaliae) with thickened margins, which could help the nymphs to keep their body in water, and the larger last pair of gills could serve as oars.



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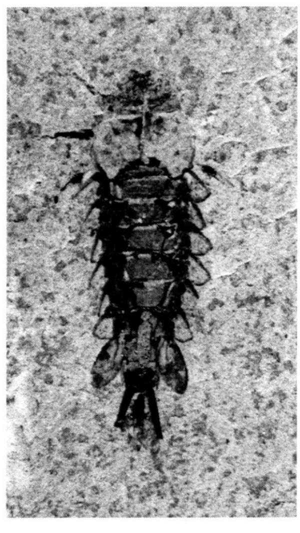

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Fig. 11-12. Aquatic insects from the Early Cretaceous of Siberia, Russia. 11 – a specialized nectic beetle larva *Coptoclava longipoda* PING 1935, Coptoclavidae; 13 – mayfly larva *Protoligoneuria limai* DEMOULIN 1955, Hexagenitidae, Early Cretaceous of Brazil.

In the Early Tertiary the lacustrine insect fauna for a long time remained poor and uniform, like in the Late Cretaceous. This is a universal pattern in all types of lakes, small as well as large and lowland as well as montane. That times the main environments of aquatic insect evolution were likely the running waters. A recolonization of lakes was slow, and diverse lacustrine assemblages are reappearing in the fossil record not earlier than near the Eocene/Oligocene boundary.

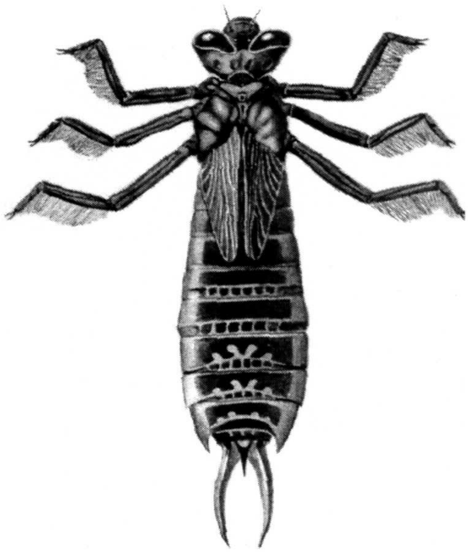

Fig. 13. Nectic dragonfly larva *Hemeroscopus baissicus* PRITYKINA 1977, Hemeroscopidae, Early Cretaceous of Siberia, Russia (reconstruction after PONOMARENKO 1980).

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