

Some Characteristics of the Trichoptera Distribution in the Mesozoic of Eurasia (Insecta: Trichoptera)

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Abstract—The stratigraphic distribution and peculiarities of burial of caddis cases from 293 Mesozoic localities in Eurasia are analyzed. An attempt is made to analyze and interpret the co-occurrence of trichopteran cases and adults in the major localities. The main stages in the evolution of the building behavior of trichopteran larvae in the Mesozoic have been elucidated.

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INTRODUCTION

Caddisflies are small or medium-size insects with an aquatic larval stage. Although this group has never been particularly diverse, caddisflies are known and relatively abundant beginning from the Early Permian. The adults are aphagous, while the larvae are predators, detritivores, or herbivores in a variety of aquatic habitats. Because all trichopteran larvae use gills for respiration, they can only live in water with an adequate amount of dissolved oxygen. The predaceous larvae are usually free-roaming, while other larvae often live in tubes (cases), which they build by attaching mineral or organic particles to a silken framework. More rarely, the entire structure consists of only silken threads. The cases are open at both ends and often are somewhat expanded anteriorly because the growing larva keeps adding to the anterior end of the case.

Fossil caddisfly remains are widespread in the geological record. Adults are known as inclusions in ancient resins as well as impressions on rocks. Unlike other aquatic insects, caddisfly larvae are extremely rare in the fossil record. The most common are trichopteran trace fossils, i.e., their larval cases, which are abundant in the Jurassic and Cretaceous lacustrine and fluvial deposits. The earliest fossil cases are known from the late Mid- or the early Upper Jurassic; thus, it seems plausible that trichopteran larvae did not construct portable cases in earlier times. The case-building caddisflies form 37 families in the suborder Phryganeina. Currently, these occur worldwide, but the Jurassic and Cretaceous fossils are known almost exclusively from East Asia. It is possible that fossil caddis cases may in fact have a much wider distribution, but their remains are ignored by collectors. For example, fossil caddis cases were only quite recently discovered in Korea (Lower Cretaceous, Jinju Formation; Paik,

2005) and China (Lower Cretaceous, Yixian Formation; personal communication of E. V. Bugdaeva). Relatively few cases have been found in the Wealden and Purbeckian of England (Jarzembowski, 1995, and unpublished data of I.D. Sukatsheva). They are absent in the Barremian of Las Hoyas (Spain) and have not been recorded from the Aptian of Santana (Brazil), two localities that have yielded extensive collections of fossil insects. In the Upper Jurassic and Cretaceous deposits other than East Asian localities, caddis cases have been found in the Upper Jurassic Morrison Formation (United States), the Cenomanian of Czech Republic and the United States, and in the Lower Cretaceous of Australia (see Sukatsheva, 1982, for a review of the records). In other parts of the world caddisfly larval cases occur sporadically in Paleogene and Neogene strata.

Caddisworm cases, especially those built of mineral particles, are exceptionally prone to fossilization. Most of the cases built of sand grains must have been preserved in the deposits of the water body where the larvae had lived (although, in coarse-grained deposits they can only seldom be distinguished from the surrounding sand). The cases built from animal or plant remains, or even from silk alone, are also readily preservable. Therefore, by counting caddisfly larval cases one can estimate the abundance and biomass of these insects more realistically than it is possible for other groups. The greatest number of caddisfly cases have been described from the Mesozoic of Transbaikalia, Far East, and Mongolia. A parataxonomic system has been proposed to classify these according to their building material and design. The first who became interested in caddisworm cases was the famous Russian geologist and paleontologist, Professor O.S. Vialov. While studying trace fossils in general, he began classifying trichopteran cases already since the 1960s and later (Vialov, 1973) he published an artificial system of cases,

which comprised the main indusgenera known by that time. Over 200 ichnotaxa have been described based on that classification (Vialov and Sukatsheva, 1976; Sukatsheva, 1982, 1985, 1989, 1991, 1992, 1994, 2005). In many localities the ichnotaxa substantially exceeds the taxa described based on adult remains in numbers and diversity. Apparently, this is mostly because of the greater probability of fossilization of caddisfly cases, compared to adult caddisflies, and also because some species could build multiple types of cases. It is still not possible to unite the parataxonomic and the natural classifications of Trichoptera because among the extant caddisflies similar cases can be built by larvae from different families and, vice versa, larvae of a single extant species can produce cases of different types (for example, the design can alter as the larva grows, Lepneva, 1966).

Moreover, in Trichoptera, as in some other insects with aquatic larvae, the directions of evolution are considerably different in the adults and in the immatures. The main changes are not synchronous in the adults and in the immatures. Moreover, as the fossil data accumulate, one encounters more and more cases when, in dozens of localities, a single species of adults and a single species of larvae dominated (or these were the only species recorded), but those adults and larvae are described in different families (for details see Rasnitsyn, 2002; Zherikhin et al., 2008).

Recently, Ivanov (2006) was the first to describe in detail larvae of Early Cretaceous caddisflies, including such that have been preserved inside their cases, from the Baissa deposits on the Vitim River and that belong to at least three different families. Based on their morphological characters, some of the larvae were placed in the recent families Leptoceridae and Brachycentridae, previously unknown in the fossil state before the Paleogene (Ivanov and Sukatsheva, 2002). All the adult trichopterans found here (173 specimens) belong to three other families of the suborder Phryganeina: the extinct Vitimotauliidae and Baissopheridae and the recent Phryganeidae (Sukatsheva, 1968). The same locality has yielded a huge number of empty cases (598 specimens) made of sand grains and plant fragments that, judging by the dominant group of adults, apparently belong to larvae of Vitimotauliidae. The presence of larvae displaying characters of Leptoceridae and Brachycentridae and the total absence of adults of these families may indicate that the extrapolation of the taxonomic standard of recent caddisfly larvae onto the Mesozoic is not well justified. The larvae described apparently belong to Vitimotauliidae and Baissopheridae. Their dissimilarity from the hypothetical recent analogues apparently reflects the explosive evolution of the larvae, which produced the extreme diversity in the design and composition of caddisworm cases in the Jurassic and Early Cretaceous, while the rapid evolution of adults, as documented by their impressions, began only in the Late Cretaceous (Sukatsheva, 1982, 1990). This example once again under-

scores the necessity of keeping two independent taxonomic systems for the order Trichoptera: a formal one for larval cases and a natural one for the larvae themselves and the adults.

Therefore, what the artificial classification represents is not the classification of caddisflies, but rather some trends in the evolution of the building behavior of their immatures, apparently repeated independently in different groups of the suborder Phryganeina. The complexity of the design of cases is evaluated using the index of constructive perfection (ICP), which is calculated based on the nature of the building material and the manner in which it is arranged. This index allows comparisons between assemblages of cases from different localities and reconstruction of the evolution of the larval building behavior in the Mesozoic (Vialov and Sukatsheva, 1976; Sukatsheva, 1990). It has been suggested that the building instinct becomes more sophisticated in a series of successive localities in the geological record. However, it turned out that cases with high ICP occur in some volcanogenic localities near the boundary between the Jurassic and Cretaceous, although they are absent from the majority of Neocomian localities. It has been found that the building materials used by the larvae in the Early Cretaceous attained a diversity that has never been equaled in the subsequent fossil record. These were not only sand grains, mica flakes, plant fragments, and conifer needles, but also seeds, ostracod and conchostracan shells, coprolites, and fish scales. The material was sometimes arranged in a peculiar manner, not occurring during later times.

The larvae of the extant Trichoptera are almost exclusively benthic forms. Only a few have lightweight cases, built of plant fragments, and swim near the water surface feeding on pleuston. The diversity of facies in which fossil cases occur suggests a great diversity of their habitats and life modes. In oxbow deposits, caddisfly cases are often found side by side with bivalves and horsetail root nodules; this suggests a shallow, well-aerated water basin. Small water bodies on inclined floodplains represented a similar type of habitats. Fossil localities of this type are known in the Wealden and Purbeckian of England.

In deposits of large lake basins caddisfly cases are encountered in small water bodies appearing at the periphery of proluvial cones. Such waters are also well aerated but relatively ephemeral; thus bivalves are uncommon here, while ostracods and, to a lesser degree, conchostracans, are more common. Like caddisflies, those two groups of crustaceans were capable of rapid colonization of water basins. In the Mesozoic, due to intensive erosion, the shores of a lake basin after it was filled with water quickly became flat, and algal platforms appeared, where an active precipitation of carbonates from the easily warmed-up water was taking place. In the deposits of carbonate platforms, caddis cases seldom occur, although several cases of their

mass burial here are known. They are significantly more common in bioherms, i.e., stromatolite-like structures, which may contain embedded caddis cases as one of their major components. The cases preserved in the carbonates after the larvae had left have been interpreted as worm tubes (Sochava, 1977). Recently, a highly interesting life mode of trichopteran larvae on stromatolites has been described from the Lower Cretaceous of Jahyeri in Korea (Paik, 2005). The cases are preserved as tight groups, oriented vertically, and they were already embedded into the stromatolite when the larvae were alive. Apparently, the latter led a sessile life and were not capable of feeding in the usual manner, i.e., by scraping algae off the surface of the stromatolite.

Yet, the majority of the Mesozoic caddis cases are buried not in the oxyphilic nearshore littoral conditions, but in deposits of the deeper, profundal zones of lake basins, including black bituminous shales, apparently formed in the anoxic lake areas poisoned by hydrogen sulfide (Yakovlev, 1968). Caddisfly larvae were not capable of living in such bottom environments. The same fossil assemblages contain remains of fish and shells of the gastropod *Gyraulus*. The fine-grained nature of the sediments contradicts the hypothesis that the cases were transported by bottom currents. Moreover, there are no signs of the cases or other remains having been dragged along the bottom. If the cases were transported from shallow-water areas, on the transects of lacustrine sediments, the density of the fossils would decrease with the distance from the shore, and they would also become sorted by their hydrodynamic properties, neither of which is observed. The hypothesis that the cases containing dead larvae floated up due to the accumulation of gases produced by decomposition and were subsequently transported by surface currents is open to the same objections. More likely, the larvae lived upon floating aggregates (algal mats), and their cases sank to the bottom when these disintegrated (Ponomarenko, 2007). The small organic remains became trapped on the surface of the thermocline and eventually decomposed by sulfur-reducing bacteria, while heavy caddis cases, dead fish, and mollusk shells sank across the boundary between water masses. This accounts for the stratigraphically important characteristic of the caddis cases: their presence in the strata essentially devoid of fossils.

Having finished with general considerations, we now turn to a more detailed analysis of the taxonomic composition of caddis cases from localities representing various ages, sedimentation types, and faunal assemblages. For this analysis quantitative characteristics of the aquatic insect faunas were obtained for 293 Jurassic and Cretaceous localities in Siberia, the Russian Far East, and Mongolia (Table 1). It is important to keep in mind that, for the time period under consideration (J_2 – K_2), two temperature maxima are hypothesized: one at the end of the Jurassic and another

between the Barremian and the Early Albian, reaching its peak during the Aptian (Krassilov, 1985).

Below, the stratigraphic distribution of insect-bearing deposits containing caddis cases is briefly characterized as it is traditionally interpreted in paleontological studies. Unfortunately, the most commonly accepted stratigraphy of the Upper Mesozoic of Mongolia (*Stratigraphy ...*, 1975) cannot be used, because it assigns the same age to similar developmental stages of lakes of different age (Ponomarenko, 1987). The Early Cretaceous lacustrine fauna of Mongolia was changing rather slowly; the typical Mesozoic families of aquatic insects persisted until the Albian. As a result, similar stages of succession of lakes of different age are often similar, both in lithology and in the assemblages of fossil aquatic animals. Terrestrial insects were changing much faster; they accounted for the drastic change of the fauna composition in the Cretaceous. In the Early Cretaceous more than half of all insects represented families that are now extinct, by the Middle Cretaceous this proportion dropped to less than 5%, while the remaining families have survived into recent times. During this change, the same or similar species appeared throughout the territory located between Transbaikalia and China, thus allowing correlation between deposits of remote regions (Eskov, 2002).

The longest succession is known for Mongolia. In the eastern and central Mongolia these are the terrigenous sedimentary, terrigenous carbonate, and coal-bearing strata of the Bakhar Formation (late Middle to early Upper Jurassic), the normal sedimentary Ulan-Ereg Formation (Upper Jurassic), the volcanogenic sedimentary Ulughei (Jurassic/Cretaceous boundary) and Tsagan-Tsab Formations (Lower Neocomian), the normal sedimentary Mogotuin, Anda-Khuduk, Shin-Khuduk (Khukhtyk) formations (Upper Neocomian), the volcanogenic sedimentary and normal sedimentary Bon-Tsagaan Formation (Aptian), and the normal sedimentary Nemegetin Formation (Maastricht). The deposits containing the large isophlebiid dragonflies are considered to be the terminal Jurassic, and deposits with the giant *Ephemeropsis* mayflies, later disappearing, the terminal Cretaceous. In the southwestern Mongolia, where the fossil insect assemblages are strongly different, caddis cases have been found in the Shar-Teg (lower Upper Jurassic) and Gurvan-Eren formations (lower Neocomian).

For Transbaikalia we accept the existing stratigraphy (Sinitza, 1975, 1993a; personal communication of S.M. Sinitza), except that the Unda/Daya deposits are considered the terminal Jurassic, based on the presence of isophlebiids, and the Turga deposits are considered the Lower Cretaceous, based on the presence of *Ephemeropsis*. The assemblages of fossil insects in the Kuti deposits are similar to those in Turga: neither contain the taxa characteristic of the Aptian deposits of Bon-Tsagaan. The Kuti deposits are only slightly younger than the Turga deposits: however, they contain

Table 1. The major localities of fossil caddisflies (Trichoptera) (Middle Jurassic to Upper Cretaceous of Siberia, Russian Far East, and Mongolia)

Region	Localities	Formation/age	Region	Localities	Formation/age
Mongolia	Bakhar	Bakhar/J ₂	Transbaikalia	Glinyanka	Glushkovo/J ₃
	Shar-Teg	Shar-Teg/J ₃		Daya	Glushkovo/J ₃
	Khutuliin	Ulughei/J ₃ -K ₁		Savina	Glushkovo/J ₃
	Khutel-Khara	Tsagan-Tsab/J ₃ -K ₁		Unda	Glushkovo/J ₃
	Tsagaan-Suburga	Tsagan-Tsab/K ₁		Chernovskie Kopi	Doronino/J ₃
	Tsagaan-Tsab	Tsagan-Tsab/K ₁		Ust'-Kara	Ust'-Kara/J ₃ -K ₁
	Anda-Khuduk	Anda-Khuduk/K ₁		Argun'-Klyuchi	Godymboi/K ₁
	Khobur	Anda-Khuduk/K ₁		Onokhoi	Godymboi/K ₁
	Bayan-Munkh	Dorogot/K ₁		Serebryanka	Gidari/K ₁
	Devseg-Bulag	Dorogot/K ₁		Pavlovka	Gidari/K ₁
	Tsavcharyn-Gol	Dorogot/K ₁		Karabon	Gidari/K ₁
	Bon Tsagaan	Bon Tsagan/K ₁		Beklemishevo	Tignya/K ₁
	Boro-Nuru	Gurvan-Eren/K ₁		Domna	Tignya/K ₁
	Gurvan-Eren	Gurvan-Eren/K ₁		Bukachacha	Bukachacha/K ₁
	Myangad	Gurvan-Eren/K ₁		Strelnikovo	Alchan/K ₁
	Guchin-Uus	Anda-Khuduk/K ₁		Utan	Utan/K ₁
	Modon-Uusu	Manlay/K ₁		Atamanovka	Turga/K ₁
	Tamir	Bainzurkhe/K ₁		Garda	Turga/K ₁
	Ulan-Tologoi	Mogotuin/K ₁		Durulgui	Turga/K ₁
	Khabtagai-Ula	Mogotuin/K ₁		Karaksar	Turga/K ₁
	Manlai	Mogotuin/K ₁		Makkaveevo	Turga/K ₁
	Khashat	K ₁		Polosatik	Turga/K ₁
	Khan-Khongor	K ₁		Semyon	Turga/K ₁
	Kholbotu-Gol	Undur-Ukhin/K ₁		Turga	Turga/K ₁
	Erdeni-Ula	Undur-Ukhin/K ₁		Shavyrtui	Turga/K ₁
	Khoutyn-Khotgor	Ulan-Ereg/K ₁		Urulyungui Depression	Kuti/K ₁
	Khurilt	K ₁		Dosatui	Kuti/K ₁
	Shand	K ₁		Duroi	Kuti//K ₁
	Shar-Tologoi	Shar-Tologoi/K ₁		Kailastui	Kuti/K ₁
	Shin-Khuduk	Shin-Khuduk/K ₁		Kuti	Kuti/K ₁
	Edrengin-Ula	Dushiulin/K ₁		Urtui	Kuti/K ₁
	Ergeneg-Ula	Dushiulin/K ₁		Kharanor	Kuti/K ₁
	Bamba-Khuduk	Nemegetin/K ₂			
Khotont	J ₃ -K ₁				
Buryatia	Uda	Uda/J ₃	Other regions	Khasyn (Magadan)	Khasyn/K ₁
	Baissa	Zaza/K ₁		Oyun'-Khaya	Eksenyakh/K ₁
	Butui	Zaza/K ₁		Khetana	Emanra/K ₁
	Zaza	Zaza/K ₁		Kempendyai	K ₁
	Malyi Amalat	Zaza/K ₁		Palets	Frantsevka/K ₁
	Romanovka	Zaza/K ₁		Syndasko	Ognevka/K ₁
	Khasurty	K ₁		Khysekha	K ₁
				Klyuch Neblizkyi	K ₂
				Darbaza	Darbaza/K ₂
				Amka	Amka/K ₂
				Buralkit	Amka/K ₂
				Arzamasov Klyuch	K ₂
				Arkagala	K ₂
				Arkharu	K ₂
				Gospitalnyi	Samarga/K ₂
		Kzyl-Zhar	K ₂		
		Bogopol'e	Bogopol/K ₂		
		Kim	Bogopol/K ₂		
		Ustinovka	Bogopol/K ₂		
		Chepi	Samarga/K ₂		

Table 1. (Contd.)

Region	Localities	Formation/age	Region	Localities	Formation/age
Transbaikalia	Bol'shoi Korui	Kalgan/J ₂₋₃			
	Mogzon	Uda/J ₃			
	Bukukun	Bukukun/J ₃			
	Bolboi	Byankino/J ₃			
	Onokhovo	Leskovo/J ₃			
	Leskovo	Leskovo/J ₃			
	Bichektui II	Ukurei/J ₃			
	Kangil	Ukurei/J ₃			
	Shev'ya	Ukurei/J ₃			
	Talangui	Tergen/J ₃			

quite different facies. There are reasons to believe that the legendary Baissa locality in Buryatia are younger than the Turga and Kuti but older than the Bon-Tsagaan deposits. However, there exists another opinion: based on the hymenopteran assemblages, Baissa has been correlated with the Purbeck deposits (Berriasian) (Rasnitsyn et al., 1998). In Transbaikalia the continental Mesozoic deposits are represented by four major subdivisions: the Shadron Group (Mid- to Upper Jurassic)–the Unda-Daya Group (Upper Jurassic)–the Turga Formation and formations of the same age (lower Neocomian)–the Kuti Formation and formations of the same age (Neocomian).

Each of the above subdivisions is characterized by multiple index species from various groups of organisms. Local groups and formations have been designated in various structural and facial regions of Transbaikalia. Most of these are of the same age as one of the above four subdivisions, and their deposits contain either the same index species or chronologically interchangeable species. Therefore, we will be using the term “biostratigraphic horizon,” employed in the *Atlas of the Paleozoic–Mesozoic Flora and Fauna of Transbaikalia* (Starukhina, 2002). Fossil assemblages of the above four subdivisions characterize the corresponding biostratigraphic horizons.

Among the four biostratigraphic horizons of Transbaikalia, caddis cases have not been found only in the Shadron Group. However, in a section of the Lower to Mid-Jurassic locality Bol'shoi Korui from the older, Kalgan Formation, 516 of 520 insect remains are unusually-shaped caddis cases of the formal genus *Scyphindusia*, similar to the pupal cases built by the recent Hydroptilidae (Table 1 and Pl. 1, fig. 12).

In East Siberia, Amur River region, and Primorye, caddis cases have been found in deposits varying in age from the Aptian to the Neogene. The most important here are Mid-Cretaceous deposits of the Sea of Okhotsk and Amur River regions and deposits in the Amur River region belonging to the Cretaceous/Paleogene boundary, which are poorly characterized in Mongolia and Transbaikalia.

The time period between the end of Jurassic and the end of the Cretaceous can be considered a unique stage in the evolution of the Trichoptera. It is characterized by a relative scarcity of fossil larvae and adults combined with a high diversity of fossil cases. The most ancient caddis cases found in the Upper Jurassic of the United States (Colorado) and the second half of the Jurassic of Mongolia (the localities Bakhar, Khoutyn-Khotgor, and Shar-Teg) comprised only 1–5% of the total number of insect remains. These localities lack full-fledged caddis case faunas, typical of the Cretaceous deposits; the cases are present here as an insignificant addition to the fossil insect assemblages. The most ancient cases have been found at Bakhar, where the insect-bearing strata are thick and include heterogeneous facies. Different facies contain different fossil assemblages. Caddis cases have been found in the middle part of the section, at the top of the Togo-Khuduk and the bottom of the Ortsog strata. These are deposits of small lakes with forested shores, abundant supply of clastic material, copious plant remains, and thin coal beds (Sinitza, 1993b). The total of 266 trichopteran remains have been found here, including four adults of the family Philopotamidae, the recent representatives of which do not build portable cases at the larval stage. The cases of *Terrindusia*, composed of mineral particles, comprise 82%. The other cases, which contain plant fragments as well, are referred to *Folindusia*. The composition of caddis cases at this locality does not differ essentially from the Early Cretaceous assemblages with low ICP. The co-occurrence of caddis cases and adults of Philopotamidae, which now build no cases, is paradoxical and remains enigmatic.

At the Upper Jurassic Lagerstätte Shar-Teg, known for the remarkable diversity of insect fossils (5000 specimens) (Gubin and Sinitza, 1996), caddisflies are few in number (3%) but occur in many horizons of the gray Shar-Teg sequence. Despite focused search efforts, no caddis cases have been found in the overlying, red, Ulan-Malgait sequence. The absence of cases in the deposits of this shallow well-aerated lake of significant productivity, as evidenced by vertebrate fossils, appears bizarre. From the Shar-Teg sequence, both

adult caddisflies (20 specimens of Philopotamidae, 1 Hydrobiosidae, and 1 case-building Dysneuridae) and larval cases (115, representing five indusigena, predominantly *Folindusia*) have been recorded. In general, the aquatic insect fauna of Shar-Teg appears unambiguously Jurassic, except for the relatively high diversity of caddis cases and the predominance of *Folindusia*, both rather more typical of the Lower Cretaceous. All the insects at Shar-Teg, including trichopteran, have been found in lacustrine deposits. Moreover, the remains of the insect larvae with gills (stoneflies, mayflies, caddisflies, and corydalids) occur in the most fine-grained deposits of the profundal. Apparently, most aquatic insects here were not benthic, but lived upon some floating substrate. Judging from the macrofossils, these could have been floating aggregates of the *Limnionia* clubmosses and *Thallites* liverworts, additionally colonized by various algae. Some of the caddis cases found at Shar-Teg are built of the *Limnionia* megaspores.

The next in time is the Khotyn-Khotgor locality (Ulan-Ereg Formation, Upper Jurassic), where larvae of isophlebiid dragonflies already occur. Here caddis cases have been found in various facies, including the black thin-layered deposits of the profundal, which are rich in organic matter. The cases comprise 8% of the entire fossil assemblage, among which 77% are *Terrindusia*, 14% are *Folindusia*, and 7% are *Ostracindusia*. The adults are represented by the family Vitimotauliidae (the genus *Multimodus* Suk., 10 specimens), previously known from the Upper Jurassic–Lower Cretaceous of Transbaikalia and China.

In the volcanogenic sedimentary rocks of Mongolia and Transbaikalia caddis cases are absent during most of the Upper Jurassic. Only four fossil adults have been found in localities of the Uda Formation in Buryatia and Transbaikalia (Uda and Mogzon; Table 2): Necrotauliidae (2), Baissoferidae (1), and Rhyacophilidae (1), among which Baissoferidae are considered case-building (Table 2).

In the localities of the terminal Jurassic–basal Cretaceous, caddis cases appear also in the volcanogenic sedimentary deposits of Transbaikalia and Mongolia. Already 823 cases (62% of all insect fossils) have been recorded from Khutulii in southern Mongolia. This locality is considered Late Jurassic, based on the presence of isophlebiid dragonflies in its lower, normal sedimentary part. In the overlying massive tuffaceous argillites, the aquatic beetles *Coptoclava longipoda* Ping, characteristic of the Cretaceous, are present (for some reason, represented exclusively by adults). Numerous remains of the floating moss *Bryokhotulinia jurassica* Ignatov appear further up the section. Mosses are absent in the lower part of the section, but eventually they appear and become abundant. The caddis cases here are built mainly from fragments of these mosses. Later yet, the lake becomes filled with volcanic ash, which produced the Mushugai fluorite and rare-

earth deposits (Sinitza, 1993b). The vast majority (ca. 770 of 823) of the caddis cases have the appearance typical of the Upper Jurassic and Lower Cretaceous (ICP = 30–40). Their composition is mixed, dominated by either uniform-sized sand grains and mica flakes, or more or less horizontally arranged fragments of plant detritus alternating with areas of bare silken threads. Sometimes the case is built of silk without any mineral encrustation. Similar size and shape of most cases, as well as the similar arrangement of the encrusting particles, and the presence of intermediate types all indicate that the cases have been built by larvae of a single trichopteran species, which used those building materials that were available. Additionally, 50 caddis cases of the *Folindusia* (*Echinindusia*) *undae* Vial. et Suk., 1976 type (ICP = 200–250) have been recorded. By the end of the lake's life its water became warm or chemically altered in such a way that it became unsuitable for its inhabitants. As photosynthesis ceased, the gas bubbles keeping the moss aggregates afloat disappeared, and the moss, together with the caddis cases, sank to the bottom. Some of the dying larvae managed to leave their cases; it is the only known instance in the geological record when the larvae became preserved at the end of a short track leading away from the case.

In the Cretaceous, the diversity and abundance of trichopteran remains, particularly caddis cases, increases significantly. All the types of cases known in the recent fauna had already existed at that time; some localities contain up to 10–15 ichnospecies. In contrast, most of the adult remains do not yet belong to recent families (Sukatsheva, 1982, 1990).

Some of the Jurassic sections in Transbaikalia, collectively called the Unda-Daya Horizon, display a complex paragenesis of volcanic products and sediments (from argillites to conglomerates), mostly of limnic genesis. The strata are rhythmic, filling out isolated depressions or parts of volcano-tectonic depressions. For these sections, temporary volcanic basins (from caldera lakes to lakes in alluvial cones, periodically covered with volcanic ash), inhabited by short-term inhabitants and surrounded by vegetation consisting of horsetails, have been reconstructed.

Like all other mentioned horizons, the Unda-Daya Horizon is characterized by a particular assemblage of caddis cases. The index species here is *Folindusia* (*Echinindusia*) *undae* and other formal species with similar case design. Below we will discuss this unusual assemblage, which includes cases with high ICP, atypical of that time, in more detail (Table 3).

The assemblages of caddis cases in different horizons are usually characterized by their average ICP (Sukatsheva, 1982). However, primitive designs with low ICP existed for very long periods of time, not only until the Upper Cretaceous, but also through the Cenozoic. Therefore, for stratigraphic purposes such cases are insufficiently informative. Fossil assemblages of cases can be characterized more accurately by their

apparent analogues (the localities Unda, Daya, Zmeinyi, Olov, Savina, Lugovaya, Shev'ya, Glinyanka, and Khilok), where *F. (E.) undae* and similar species occur in large numbers (Table 3). In general, the fossil assemblages of the Unda-Daya Horizon are characterized by a dramatic prevalence of caddis cases built of plant fragments. Apparently, this is explained by lack of a significant influx of terrigenous material into basins inhabited by caddisflies, rapid burial of sand by finely dispersed ash, and abundance of plant material. Analogous deposits in Mongolia (Khutuliin, J₃–K₁) also contain caddis cases of the *F. (E.) undae* type. In the basal Cretaceous, cases built of plant material are known from the Khasurty locality. Further up they have been found in the Neocomian (Kuti, Kailastui) and the Albian (Khetana). Therefore, the cases of *F. (E.) undae* are the most widespread in the Upper Jurassic of Transbaikalia. Also relatively common here are cases built of plant particles arranged according to the *F. (E.) undae* type, but differing from the latter in some formal characters. In the Upper Jurassic to Lower Cretaceous and in the Neocomian such cases are much more common than *F. (E.) undae* itself. In the rich Transbaikalian locality Semyon, despite the large size of available collections, cases of the *F. (E.) undae* type have been found only sporadically. These deposits are often correlated with the Turga Formation in eastern Transbaikalia and with its Mongolian analogues (Bugdaeva, 1983), although some authors estimated their age to be as early as Aptian or Albian (Srebrodolskaya, 1973). Yet, the fish fauna at this locality differs profoundly from the ichthyofauna of the Turga Formation (E. K. Sychevskaya, personal communication). Semyon also differs from other Turga localities in the composition of some insect groups represented here. For example, when beetles are considered, Semyon stands out sharply in the high abundance of cupedids and scarabeids. Dragonfly and hymenopteran remains are much more frequent here than in localities of the Turga Formation. At Semyon, the caddis cases of the *F. (E.) undae* type occur together with other types of cases, which also have high ICP (= 150) but never occur in the Turga faunas. In the younger deposits (the Kuti, Kailastui, and Khetana localities), neither *F. (E.) undae*, nor similar caddis cases occur, although the cases made of plant material are common. Currently, there is no clear explanation of this distribution. It is particularly odd because, at all of the above sites, the cases are similar yet they vary somewhat in their size and the nature of the building material.

Among faunistically interesting localities not containing cases of the *F. (E.) undae* type, three more Upper Jurassic or Upper Jurassic–Lower Cretaceous localities are noteworthy: Kempendyai, Chernovskie Kopi, and Khotont, where the fossil aquatic fauna is particularly abundantly represented. At Kempendyai, trichopterans comprise 20% of all insect remains, including several adults (3 Philopotamidae, 2 Dysonauridae, 1 Necrotauliidae, and 6 Polycentropodidae) and

Table 3. Distribution of caddis cases of the *Folindusia (Echinindusia) undae* type

Age	Localities	<i>F. (Ech.) undae</i>	<i>F. (Ech.) near undae</i>	<i>F. necta</i>	<i>F. (Ech.) kailastuica</i>	<i>F. (Ech.) exculta</i>	<i>F. (Ech.) lebedevi</i>
K ₁	Khetana						
	Kuti						
	Kailastui						
	Semyon						
	Gusinoe Ozero						
	Khasurty						
	Khilok Depression						
J ₃ –K ₁	Khutuliin						
J ₃	Bolboi						
	Unda						
	Glinyanka						
	Shev'ya (Kuenga)						
	Zmeinyi						
	Savina						
	Olov						
	Daya						
	Lugovaya						

a large number of *Folindusia* cases. At Chernovskie Kopi, adults (1 Phryganeida, 1 Dysonauridae, 1 Calamoceratidae, 1 Plectotarsidae, and 7 unidentifiable wing fragments) and a large number of cases, almost exclusively *Folindusia*, have been recorded. At Khotont, only three caddis cases have been found. At both Kempendyai and Chernovskie Kopi, the constructive perfection of the cases suggests the Neocomian age, while the composition of adult remains is completely unique because neither Calamoceratidae, nor Plectotarsidae occur elsewhere in Transbaikalia at that time period, being recorded only from the Lower Cretaceous of England (Purbeck Limestone Group) (Sukatsheva and Jarzembowski, 2001).

In the Lower Cretaceous, caddis cases occur both in normal sedimentary rocks and in volcanogenic sedimentary rocks. Two Lower Cretaceous horizons can serve as examples.

The volcanogenic sedimentary Turga Horizon (alluvial and lacustrine facies combined with proluvial facies along the rims of depressions) is characterized by a large diversity of habitats and the fauna that is, in general, more ordinary than that of the sections of the Unda-Daya Horizon. Both the building materials of the caddis cases and, consequently, the cases themselves

Explanation of Plate 5

Fig. 1. *Terrindusia (Terrindusia) notabilis* Suk., 1993, PIN, no. 3800/1006; Khabarovskii Krai, Khetana; Lower Cretaceous, Albanian; a caddis case built of terrigenous materials, mostly mica flakes, $\times 5.7$.

Fig. 2. *Pelindusia conspecta* Vjal. et Suk., 1976, PIN, no. 1717/54; Buryatia, Romanovka; Lower Cretaceous; a caddis case built of mica, $\times 4.0$.

Fig. 3. *Indusia incredibilis* Suk., 1990, PIN, no. 4180/24; Chita Region, Karkasar; Lower Cretaceous, Turga Formation; a caddis case built of plant material with addition of ostracod shell fragments and coated on the outside with mollusk shells, $\times 3.0$.

Fig. 4. *Folindusia (Acrindusia) indecens* Suk., 1993, PIN, no. 3800/984; Khabarovskii Krai, Khetana; Lower Cretaceous, Albanian; a caddis case built of plant material with addition of sand grains, $\times 3.3$.

Fig. 5. *Folindusia (Acrindusia)* sp., PIN, no. 4288/913; Mongolia, Khutuliin; Upper Jurassic-Lower Cretaceous, Ulughei Formation; a caddis case built of plant material with addition of mica flakes, $\times 4.0$.

Fig. 6. *Folindusia (Folindusia) peridonea* Suk., 1982, PIN, nos. 3800/1-6; Khabarovskii Krai, Khetana; Lower Cretaceous, Albanian; caddis cases built of plant material, $\times 1.7$.

Fig. 7. *Secrindusia admiranda* Suk., 1982, PIN, no. 3064/1008; Buryatia, Baissa; Lower Cretaceous, Zaza Formation; a caddis case built of secretory material with addition of sand grains, $\times 3.3$.

Fig. 8. *Folindusia (Folindusia) palmaris* Suk., 1993, PIN, no. 3800/823; Khabarovskii Krai, Khetana; Lower Cretaceous, Albanian; a caddis case built of plant material, $\times 5.5$.

Fig. 9. *Folindusia (Folindusia)* sp., PIN, no. 4288/1162; Mongolia, Khutuliin; Upper Jurassic-Lower Cretaceous, Ulughei Formation; a caddis case built of plant material, $\times 4.3$.

Fig. 10. *Folindusia (Acrindusia) malefica* Suk., 1982, PIN, no. 3799/1; Khabarovskii Krai, Amka; Upper Cretaceous, Cenomanian, Amka Formation; a caddis case built of plant material, $\times 5.5$.

Fig. 11. *Folindusia (Folindusia) undae* Vjal. et Suk., 1976, PIN, no. 1857/7; Chita Region, Unda; Upper Jurassic, Glushkovo Formation; a caddis case built of plant material, $\times 5.0$.

Fig. 12. *Scyphindusia hydroptiliformis* Suk., 1985, PIN, no. 4009/43; Chita Region, Bol'shoi Korui; Middle to Upper Jurassic, Kalgan Formation; a caddis case built of secretory material, $\times 8.0$.

show the greatest diversity here. Fragments or whole shells of ostracods, bivalves, gastropods, conchostracans, as well as plant seeds occur here as main or accessory building materials of the cases. Virtually all formal genera and subgenera known in the Mesozoic of Asia, particularly those including cases built of organic materials, appear here. The Turga caddis cases have been divided into several assemblages, arranged from the bottom to the top (for details see Sukatsheva, 1990). The subdivision is based on the dominant species and also takes into consideration the stratigraphic relationships between particular sections. Particularly important here are the cases made of plant fragments (*Folindusia* s. str.) or animal materials (*Ostracindusia*).

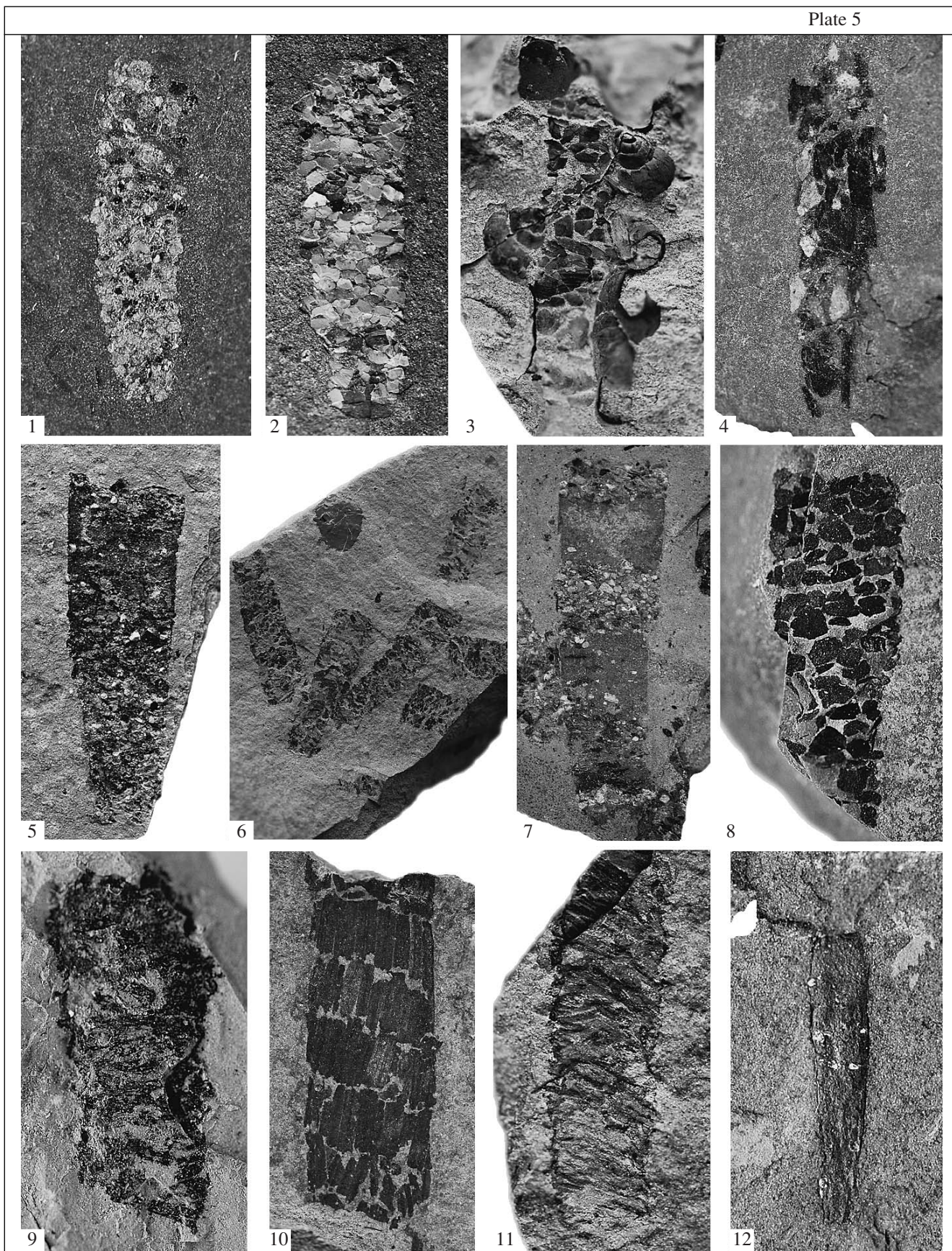
The Kuti Horizon is characterized by coal-bearing rocks filling out troughs within consedimentation depressions: the channel and alluvial-proluvial facies, floodplain deposits, or, more rarely, the deposits of river channels, floodplain or bog lakes, oxbow lakes, and marshes. Signs of volcanic activity are absent; the transition between coal-free and coal-bearing strata can be observed in the sections. The caddis case assemblages here have been established based on the same principles as for the Turga Horizon. The difference is in the mass appearance of the cases built of conifer needles and the wide distribution of the cases built entirely of mica flakes. On the other hand, the number of the cases built of animal materials is much lower. In other words, in both horizons, the proportion of caddis cases with chaotically arranged particles (i.e., the subgenera *Profolindusia* of the genus *Folindusia* and *Mixtindusia* of the genus *Terrindusia*) is decreased in the upper parts. The maximum diversity of the cases built of organic mate-

rial is observed in the Turga Horizon. Moreover, the proportion of mica in the building material increases. In the Kuti Horizon, the cases built entirely of mica flakes occur in large numbers.

For a more precise characterization of the faunal composition of the cases we will consider a few specific examples. In the Late Cretaceous, the cases also occur in both the normal sedimentary and the volcanogenic sedimentary rocks. Yet, they relatively seldom become preserved together with remains of aquatic insects, because the rich lacustrine insect fauna typical of the Jurassic and Early Cretaceous becomes virtually extinct by the Middle Cretaceous (Kalugina, 1974; Zherikhin, 1978). As a result, many Upper Cretaceous localities contain only caddis cases (Darbaza, Buralkit, Bamba-Khuduk, Bulun, Amka) or caddis cases together with beetles (Arzamasov Klyuch, Arkagala, Bogopol, Kim, Ustinovka, Ero-pol, Mukha). It is quite surprising that caddis cases are absent in the localities Obeshchayushchyi (Cenomanian) and Obluch'e (Santonian), although the insect remains collected there are quite numerous (1202 and 25 specimens, respectively). In the few Upper Cretaceous localities of the Amur Region the insect fossils are neither particularly abundant, nor diverse. This is also true of caddis cases. For example, no more than 20 insect specimens are known from the locality Udurchukan (Campanian). These include very typical, large cases of *Folindusia (Acrindusia) kodrulae*, built of plant material (Sukatsheva, 2005). Similar cases have been found in the Arkhara-Boguchan coal open-pit mine (Danian).

The analysis of the Upper Cretaceous caddisfly faunas (Sukatsheva, 1991) is easily interpretable in the

Plate 5



framework of the knowledge on the evolution of lake ecosystems (Ponomarenko, 2007). The Early Cretaceous corresponds to the stage of a rapid evolution of the larval building behavior, and the Late Cretaceous to the equally rapid radiation of adults of the suborder Phryganeina into numerous families, apparently resulting in the appearance of the majority of recent families (Sukatsheva, 1982; Botosaneanu and Wichard, 1983; Zherikin and Sukatsheva, 1990).

Having discussed some specific age-related and faunal characteristics of assemblages of fossil caddis cases, we will now turn to some general patterns of their burial.

Our study of the composition of the aquatic insect faunas at the 293 localities reviewed has demonstrated that, if the caddis cases appear as part of small collections, then they usually either dominate, or occur together with beetle remains in the localities taphonomically unfavorable for preservation of insects with a thin integument. At the localities with normal taphonomic conditions, the cases are usually rare, which is typical of regular aquatic communities. Sometimes their proportion reaches up to 20–70% of the entire fauna (Khutuliin, Bon-Tsagaan, Vitim, Durulgur, Devsegbulag, Kholbotu-Gol, Shand, Shar-Tologoi, Shin-Khuduk, Erdeni-Ula, Malyi Amalat, Romanovka, Glin-yanka, Kangil, Karakol, Savina, Unda, Chernovskie Kopi, Garda, Pavlovka, Polosatik, Semyon, Khetana, Kholui).

In addition to taphonomic and other natural factors affecting the distribution of caddis cases, one should also take into consideration the human factor. For a long time geologists and paleontologists did not recognize and did not collect caddis cases; for many localities the available collections do not reflect the true composition of the fossil assemblages.

Our analysis of the distribution of caddis cases would be incomplete without comparing the records of the adult trichopterans with the records of the larval cases. Table 2 shows that at those localities of the second part of Jurassic (Bakhar and Khotyn-Khotgor) where both the adults and cases of trichopterans occur, *Terrindusia* dominate among the cases, while the adults belong to Philopotamidae and Vitimotauliidae. At the Upper Jurassic Lagerstätte Shar-Teg, the diversity of both indusigena and adults is much higher. In the Unda-Daya Horizon, dated as the upper Upper Jurassic, diverse caddis cases and the unique *F. (E.) undae* occur together with representatives of four different families of adults (Unda, Daya). At the somewhat younger localities Kempendyai and Chernovskie Kopi, the diversity of adults is also surprisingly high, contrasting with the sheer prevalence of *Folindusia* among the cases (> 90%). A similar picture is observed only in the Purbeck strata of England (Table 2). From the majority of Lower Cretaceous sites, only a single family of adults has been recorded. There are two exceptions to the general pattern. At the Khutel-Khara locality (K_1),

where only three poorly preserved (pupal?) cases have been found, the adult specimens belong to the two families that do not construct cases: Polycentropodidae (12) and Philopotamidae (1). At the Bichektui II locality (J_3-K_1), only one adult Polycentropodidae and three larval cases have been found. In the recent representatives of the above families immature stages do not build any portable shelters.

From the Upper Cretaceous, alongside with scarce caddis cases, adult Philopotamidae and Phryganeidae have been recorded (Arkhar, Kzyl-Zhar).

A comparison of the taxonomic composition of caddis cases and adult caddisflies from localities of the same age suggests that different case species have been built by larvae from the same families but under different ecological conditions. For example, Vitimotauliidae have been recorded both in the localities with a significant prevalence of *Folindusia* (Bon-Tsagaan, Kholbotu-Gol) and the localities where exclusively *Terrindusia* have been found (Khobur).

This is a preliminary study and it demonstrates the potential of caddis cases in solving problems in stratigraphy and paleoecology, as well as the challenges of this approach itself.

The characteristics of the caddis case assemblages, which have been discussed above, cannot be easily used for determination of the relative ages of the enclosing deposits even within the Transbaikalian region because these characteristics were produced by pooling data. Moreover, in order to use caddis cases for biostratigraphic dating (i.e., correlating specific sections), one needs to take into consideration peculiarities of sedimentation in the structural zone or facies. It is even possible that the taxonomic diversity of the cases, although varying with the age of the deposits, does not correlate with the age itself, being rather an indicator of the changing paleoecological situation.

In conclusion, the main features of stratigraphic distribution and evolution of the adults and cases of the Mesozoic caddisflies can be summarized as follows:

(1) The case-building behavior evolves in caddisfly larvae in the second half of the Jurassic, approximately at the same time when the origination of the families survived to the Recent accelerates; the latter process is generally characterized by the origin of increasingly regular arrangement of the building material and the increasing diversity of such materials.

(2) This process is not completely linear: highly sophisticated cases appeared already at the end of the Jurassic, but then they disappeared from the record in the middle of the Neocomian to reappear again in the Upper Cretaceous deposits.

(3) The second half of the Neocomian is characterized by wide use of plant and, particularly, animal materials, including those not used or only rarely used by the recent caddisflies (seeds, club moss megaspores,

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