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# Mass mutations of insects at the Jurassic/Cretaceous boundary?

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**Abstract:** Diverse fossil insect assemblages near the Jurassic/Cretaceous transition from the Shar-Teg in Mongolia comprise frequent deformed species. These (first known) mass fossil animal deformities, expressed as fusions of veins changing the wing geometry, probably represent heritable mutations. They accumulated as a result of a changed structure of selective pressure, and are unique in showing how individual variations may be fixed to form higher taxa, significantly contributing to the process of evolution. Similar deformities were also recorded in recent ecosystems undergoing elevated environmental stress. The occurrence of deformities indicate a long-lasting (100 kyr–1 Myr) ecological stress in the continental environment before the J/K boundary and a biotic character of the changes: high evolutionary tempo and consequent radiation of newly evolved taxa forming new control mechanisms including social decompositors and new predators, resulted in temporary more or less destabilized ecosystems and uncontrolled, rapid evolution of its elements. Accordingly, ecosystems with higher diversity stabilized and some of their elements remained virtually unchanged for over 30-million-years at least in Laurasia. Notably, occurrences of true flowering plants and some advanced insects during the lowermost Cretaceous are limited to the region.

**Key words:** evolutionary mechanisms, modern ecosystems, boundary events, mass mutations, deformities.

## Introduction

Variability extended by mutations, and natural selection in the widest sense (comprising factors influencing fitness and sexual selection) are essential premises for some of the evolutionary processes eventually resulting in self-organization.

Deformities of the insect wings presented in this paper provide indication of occurrence of mass mutations in certain periods such as during some boundary times when rapid evolution and/or radiation might have taken place.

It is hypothesized that during these comparatively short time sections, significant mutations might result even in the origin (and/or rapid evolution) of new higher taxa such as those at the family and/or higher rank.

The origin of new control mechanisms, including social decompositors near the J/K boundary, display strong convergence with recent activities of humans, which apparently also represent new control mechanisms, temporarily destabilizing ecosystems.

## Material and methods

170 mostly fragmentary specimens (Table 1) of geologically different age from the Upper Jurassic sediments of the Shar-Teg in Mongolia (Fig. 1) were studied: the near J/K transition dating is based on the distribution of fossil plants, gastropods, bivalves, ostracods, conchostracans, insects, chelycerates, fishes, labyrintodont amphibians, turtles, crocodiles, dinosaurs and mammals (Gubin & Sintza 1996; Vršanský 2004).

Specimens are compared with over 3000 insect specimens of Mesozoic and Paleozoic insects world-wide: results from the Carboniferous specimens from Germany and the Permian specimens from the Boskovice in Czech Republic are based on the drawings made by Schneider (1978, 1980ab, 1982) and on my unpublished observations. The figures of the Upper Triassic insects of Mady-

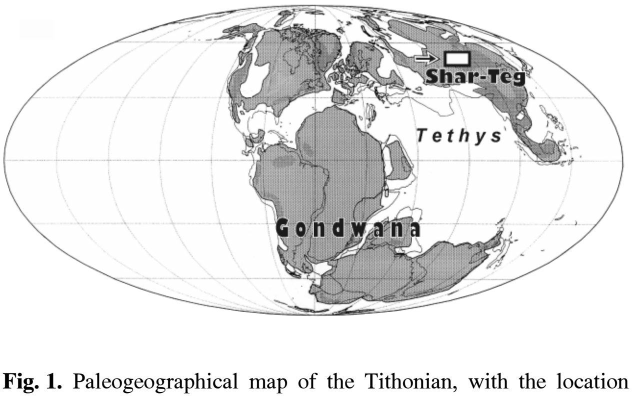

**Fig. 1.** Paleogeographical map of the Tithonian, with the location (rectangle) of the Shar-Teg in Mongolia. Notably, occurrences of all the lowermost Cretaceous assemblages with flowering plants and some advanced insects are limited to Asia — regions adjacent to Shar-Teg. Coastlines after Smith et al. (1994).

gen in Kirgizia originated from drawings made by Vishniakova (1998) and by my unpublished materials. The data obtained from Dobbertin in Germany (Late Jurassic) were based on observation by Vršanský & Ansorge (in print). The figures of the Middle Jurassic material from the Bakhar in Mongolia and the Kimmeridgian specimens of Karatau in Kazakhstan are based on my unpublished materials (in preparation). The Baissa material originates from the Berriasian or Valanginian (Lower Cretaceous) sediments of Siberia (Vršanský 1998b); figures of the Spanish material (Valanginian or Hauterivian Lower Cretaceous insects of Montsec) originate from unpublished materials (based on the material collected by J. Ansorge and X. Martínez-Delclós respectively). Mongolian material from the Bon Tsagaan (Barremian or Aptian Lower Cretaceous) has been described by Vršanský (2003).

The Shar-Teg material has been collected by the Arthropoda Laboratory, Paleontological Institute of the Russian Academy of Sciences, Russia, where it is deposited.

The contemporary material originating from Equador, Laos, Malaysia, Madagascar, Israel, Slovakia and Croatia is deposited in the Slovak National Natural History Museum, Bratislava and in the Zoological Institute, Slovak Academy of Sciences.

The wing deformities are present as teratological fusions of competent veins. These are abbreviated as: R — radial system; M — medial system; Cu — cubital system and A — anal system.

## Results

In the Shar-Teg, the deformities — which change the geometry of wings — are expressed as fusion of vein to another vein (R-M Fig. 2d–e), mutual fusion of two veins (M-M Fig. 2a or M-R Fig. 2b), lost of a (M) branch (Fig. 2c), additional branches among cross-veins (Fig. 2f), as blind veins with unfinished growth (Fig. 2g) or as widened, lentiform, veins (Fig. 2h). Fused veins are present mostly between the medial and radial systems which vein distribution is highly correlated (Vršanský 1997, 2000), or within the medial system. Unfinished growth of veins is additionally recorded within the anal system.

The deformities in fossil caddis flies are recorded as lentiform thickening of the radial vein. Appropriately named *Bullivena* Novokshonov et Sukacheva, 1995 and *Oncovena* Sukacheva et Novokshonov, 1995 (*O. sharategensis* Ivanov et Novokshonov, 1995) from the families Hydrobiosidae and Dysoneuridae respectively (Novokshonov et al. 1995) possess virtually identical types of teratology.

Thus, the wing venation deformities are recorded in primitive and derived insects. Such environmentally induced changes occur in cockroaches and mantises such as *Juramantis initialis* Vršanský, 2002, the oldest mantis known to date. Rich venation of the both groups enable tracking of the deformities in the fossil record. Cockroaches and mantids are additionally considered to be a stratigraphic tool for high temporal resolution (Vršanský et al. 2002).

Among Dictyoptera, five independent lineages were affected. Two of the family Blattulidae, namely *Blattula* Handlirsch, 1906 (*B. mongolica* Vršanský, 2004) and *Elisama* Giebel, 1856 (*E. pterostigmata* Vršanský, 2004), which are diurnal species inhabiting shorefaces. The third has been found in the Mesoblattinidae (*Mongolblatta accurata* Vršanský, 2004), which is predominantly a forest species. The fourth among the new family (*Shartegoblattina elongata* Vršanský, 2004) presumably of crepuscular habits; and lastly in the predatory mantid of the family Juramantidae (*Juramantis initialis* Vršanský, 2002). These above-mentioned occurrences indicate a great variety of niches affected by environmental stress. Of these five taxa, 8 of 69 specimens bear deformities approximating the ratio of affected individuals in the habitat to 15–20 % (the higher approximated ratio resulting from highly fragmentary material, damaged by predation (Vršanský 2004) — therefore not all deformities are preserved. For example, 17 % of all preserved roaches are represented by isolated clavi. This especially concerns larger species, where wing defor-

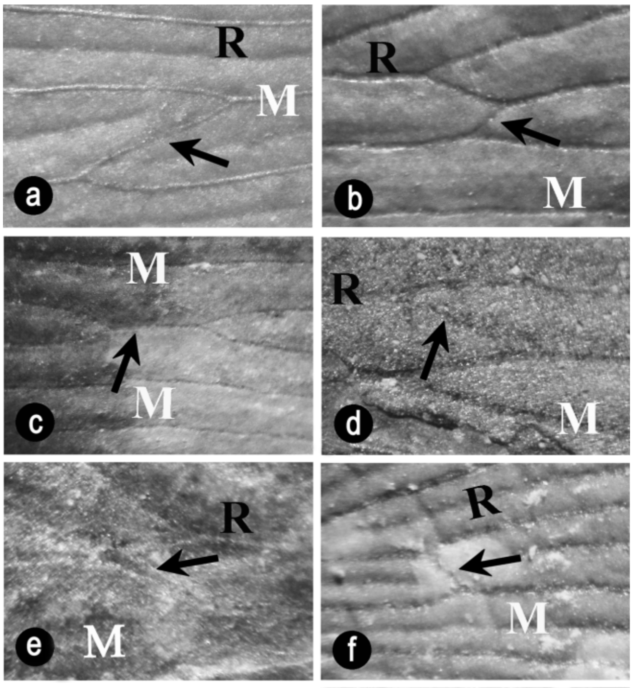

**Fig. 2.** Wing deformities from the Shar-Teg. **a–f — Cockroaches.** a — *Elisama pterostigmata* Vršanský, 2004, PIN 4270/1916; b–c — *Mongolblatta accurata* Vršanský, 2004, PIN 4270/1856; d — PIN 4270/1827; e — *Elisama mongolica* Vršanský, 2004, PIN 4270/1798; f — *Elisama pterostigmata,* PIN 4270/1835. **g — Mantis** *Juramantis initialis* Vršanský, 2002, PIN 4270/1842. **h — Caddis-fly** *Bullivena grandis* Novokshonov et Sukacheva, 1995 PIN, 4270/123. **R** — radial system, **M** — medial system, **A** — anal system.

mities occur more frequently as with the nocturnal Caloblattinidae, which are absent in the Shar-Teg assemblage. Additionally, on some wings, multiple deformities occur. The small species also change the ratio of affected individuals since damage in its wing would affect their flight abilities and thus their chance of being preserved).

## Discussion

The preserved deformities are highly variable in location and thus this mutation(s) most probably affects general regulatory control. This supports the appearance of wing deformities of different insects including cockroaches caused by the application of general growth regulator (IGR — hydroprene) (Arthur 2003). The supportive function of the fusion is insignificant because this function is provided by cross-veins.

According to Bartlett & Staten (1996), a recessive mutation and genetic changes in a single gene could lead to wing deformities and thus to decreased fitness if the gene could be forced into the native population in large numbers.

In addition to deformities, variability of undeformed cockroaches at the Shar-Teg might differ from the general trend of their decreasing variability of the total number of veins as determined by study from the Pennsylvanian to the Recent (Vršanský 2000). Consequently, it is possible that similar or identical regulatory genes are responsible for the control of regular spacing of veins, a developmental process that apparently failed in the specimens described above.

Notably the most common cockroach at the Shar-Teg lacked these deformities, which would indicate that they were not affected by environmental stress. A possible explanation for the lack of the deformities in the common species is its small size and therefore low number of veins which results in more strict selective control of each individual vein as reported for fossil cockroaches by Vršanský (1998a). Nevertheless, it is most probable that the deformity in such small individuals would influence their flying abilities and thus limit the preservation potential.

The heritable character of wing deformities is also shown by Eldon et al. (1994) from different *Drosophila* genes (e.g., mutation in 18 w resulting from improper eversion of imaginal discs).

Similar deformities affected different phylogenetic lineages, which can serve as the evidence for a stabilized and heritable mechanism for acquisition of these changes, resulting in a reduction of fitness. In such a case, these mutations of developmental genes, which are debilitating and potentially lethal, are effectively lost from populations. Such heritable wing deformities can serve as markers to important genetic traits like fitness (Suszkiw 2005).

The stability of the total number of veins at the wing margin and the constant vein number/wing surface ratio in spite of deformities since the Pennsylvanian indicates that the developmental control mechanisms during wing growth must have been evolved since the first fossil appearance of the Dictyoptera lineage.

By comparison with the Mesozoic sites, vein fusion appears more common in some Paleozoic sites such as in the Permian sediments of the Bohemian Massif, where 3 of 29 forewings are deformed, which might be facilitated by the larger size of Paleozoic cockroaches and the higher number of veins, each of lesser selective control, but also by the destabilization of the ecosystems at the beginning of the Permian. In spite of that, in the Carboniferous sediments of Germany, only 4 of 256 forewings bear deformities.

In Mesozoic localities, both younger and older than Shar-Teg, vein fusion is considerably rarer. In the Triassic sediments of Madygen in Kirgizia no deformities are recorded among more than 100 studied specimens. In the Middle Jurassic sediments of Bakhar in Mongolia only 5 of over 500 forewings bear deformities, a similar ratio is known for Eurasian Lower Cretaceous sites: 6/673 at Bon Tsagaan in Mongolia, 2/121 at Montsec in Spain and 3 of about 400 in Siberian Baissa. A comparatively higher number, even much less than those of the Shar-Teg, ratio (3/52) occurs in the Lower Jurassic sediments of Dobbertin in Germany which originated in island areas and thus characterize low diversity ecosystems destabilized to some degree (Vršanský & Ansorge in print). These occurrences appear to be supported with the data from Recent habitats (see below). Even though, fusion ratio from Shar-Teg is disproportionally high particularly for a modest diversity — 7 genera, 8 species and 170 specimens. In the more diverse Karatau in Kazakhstan of a comparable (Kimmeridgian) age, a single deformity is recorded among 668 studied specimens comprising about 60 species.

Parallel fusion and unfinished growth of veins has not been recorded throughout the 325 Myr history of the Dictyoptera. This indicates that errors in growth and failure of control in wing development represent a failure in communication between respective venial systems and individual vein systems, which normally have constant distance between veins. Although these uncommon changes affected the genetic variability of the population through enhancing the diversity of the venation pattern, the most stable taxonomic character of the wing venation — the total number of veins appears unaffected. Thus the ratio of the wing surface to the total number of veins appear constant and control of the total number of veins at the wing margin (with coefficient of variation around 5–10) was at least partially functional. Nevertheless, selective absence of deformities in smaller individuals allows a conclusion that the malformations did affect the function of the wings.

Deformities of this sort were not recorded in Dictyoptera in the intact contemporary rainforests of the Equador (0/120) and they are extremely rare (apparent as a simple fusion of veins) in primeval forests of Laos (1/272) and Malaysia (1/180). On the other hand they are common in damaged areas of the rainforests in

Madagascar (4/32), SE Asia (12/102) or deserts of Israel (10/98). It is also important that in extant desert cockroaches, as well as in the Paleozoic Blattaria, deformities are mostly restricted to larger species with an increased number of veins (and possibly reduced flight abilities), while in the Shar-Teg, they also affect small, apparently actively flying species. Partition of deformities differs even within the same modern genera — while in native forest areas of Slovakia, deformities of *Ectobius* are extremely rare (4/568), this ratio is higher in the Mediterranean (4/112).

The presence of virtually identical deformities in different lineages of caddis-flies indicates a genetic basis. Apparently, this is supported by the presence of similar structures about as stable morphotype in living Conoesucidae from Australia (Mosely & Kimmins 1953; Neboiss 1977). Only four specimens (belonging to different families) of thousands of known fossil caddis-fly species bear such structures. Two of them (of about 20 caddis-flies) belonging to different species, genera and even families are present in Shar-Teg and therefore it can be concluded they represent individual variability. Stabilization of this morphotype in a continent different to Eurasia represented by the Shar-Teg deposits may possibly indicate global occurrence of the changes and mass mutations at the whole boundary, not limited to surroundings of the Shar-Teg.

However, the appearance of virtually modern elements of ecosystems such as flowering plants and some modern insects during the earliest Cretaceous is limited to Asia, regions more or less adjacent to Shar-Teg. The Shar-Teg, where the mass mutation appeared, is the oldest locality of the Cretaceous type, which might indicate a regional character of the changes resulting in origin of modern particles of ecosystems.

Similar wing deformities indicate a similarity of Recent changes across the food web in these habitats.

The cause of the mass deformities at Shar-Teg is obscure. Volcanic activity which modified pollen (Krassilov 2003) and insects (2 of 3 cockroaches and a single preserved ice-crawler are deformed at the Nedubrovo locality in Russia) at the P/T boundary, has hardly been involved. Shar-Teg deposits do not contain any volcanic particles, minerals etc. (unpublished observation).

Similar changes of the venation are recorded for organisms in the area around the Ukrainian city of Chernobyl after the nuclear power-plant accident of April 26, 1986. Nuclear isotopic radiation affects the insect genome (e.g., Williams et al. 2001) by penetrating an insect through two relatively independent trophic chains: (1) carbon dioxide from consumption of foliar material, and graphite through the ingestion of microfungi, protozoans and other insects (Kovaliukh et al. 1998). Nevertheless, radiation as a reason for changes in the cockroach species at Shar-Teg may be excluded, attributable to the absence of an effect on species living in different time (the layers containing deformities differ in the scale of dozens of thousands years — see Table 1), the radiation needs to be global (more global than, for example, the natural reactor in Oklo which had started the fusion in a result of concentration of radioactive elements by protists. Nevertheless, nothing like that is known in history.). Notwithstanding, some Shar-Teg layers containing samples with deformities are free of radiation (e.g., the Bed 451/3), the others are slightly radioactive, most probably as a result of post-burial contamination (see Table 1). For comparison, the post-Chernobyl radiation of insects was much higher (±5.000 Bq/kg) even in the Central Sweden (Dahl & Grimas 1987). Considerably elevated radiation is necessary to modify or kill insect cells: the 80 % lethal dose for insect cells is 60 Gy (Grey) and for cockroaches 900–1000 Gy requiring weeks of exposure is necessary (Koval 1983).

Some insects retrieved from the Chernobyl event possess more significant deformities (Hesse-Honegger 2002), although if such deformities occurred at Shar-Teg, they would have affected the ability of insects to fly and thus their chance of burial.

Calibration to sediment accumulation rate shows that the Shar-Teg fossil insects are preserved in strata of slightly different age (Vršanský 2004). Age differences between successive beds are minimally 100 kyr (about 90 m). An abrupt reversal in climate change such as a pronounced change of temperature and/or aridification may have caused such ecological stress. It is notable that even short, only an hour lasting temperature shock of -10 °C is reported to cause wing deformities in flies (Milkman 1962; Hegdekar 1971; Rinehart et al. 2000). Insects are

**Table 1:** Distribution of the Dictyoptera from the Shar-Teg representing the common fauna throughout the section. Specimens with vein fusions are marked with "*". Isotopic radiation of samples: PIN 4270/1798 (451/3) — 4.4602 g — $^{238}$U less than 33 Bq/kg; $^{232}$Th less than 72; PIN 4270/1835 (443/1) — 5.3305 g — $^{238}$U 92 ± 19 Bq/kg what is ca. 7.5 ppm or 7.5 mg $^{238}$U/1kg; $^{232}$Th less than 55 Bq/kg). ?= unknown bed.

| **Species/ Bed** | **?** | **423/5** | **423/6** | **423/9** | **434/2** | **441/4** | **442/2** | **443/1** | **443/2** | **451/3** | **452/2** | **465/2** | **Total** |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Shartegoblattina elongata* | 2 | | | | 1 | | | 10–1* | 1 | 1 | 2 | | 17 |
| *Breviblattina minor* | | | | | | | | 4 | | 1 | | | 5 |
| *Mongolblatta accurata* | 1 | | 2 | | | | 1 | 13–2* | | | | 1 | 18 |
| *Elisama pterostigmata* | 5 | | 5–1* | | 1 | 1 | 1 | 14–2* | | 2 | | | 29 |
| *Blattula mongolica* | 1 | | 1 | | | | | 2 | | 1* | | | 5 |
| *Blattula vidlickai* | 3 | 1 | 7 | | 7 | 1 | | 22 | 1 | 1 | | | 43 |
| *Elisamoides mantiformis* | | | | | | | | 3 | | | | | 3 |
| gen. et sp. indetermined | | | | | | | 2 | 1 | | | | | 3 |
| *Juramantis initialis* | | | | | | | | 1* | | | | | 1 |
| Unidentifiable | 6 | | 2–1* | 2 | 3 | | | 28–2* | 4 | 1 | | | 46 |
| **SUM** | **18** | **1** | **17–2*** | **2** | **12** | **2** | **4** | **98–8*** | **6** | **7–1*** | **2** | **1** | **170** |

sensitive to temperature stress because of their small size and ectothermy. A global temperature perturbation at the Jurassic/Cretaceous boundary would have been enabled regionally by the continental crust uplift caused by the Kimmeridgian orogenesis and thus of change of monsoon currents in Asia. During intervals of prolonged aridification, deformities might have accumulated, as it is present in extant xeric habitats (see below) and also during the dry Permian Period (see above). Deformities are also common in humid areas of exploited rainforest, but exclusively in areas where the deforestation causes arid microclimate. Nevertheless, also there, the cause of deformities needs to be sought within the habitat changes rather than in common local climate changes: a long lasting climate change would probably have caused a change of fauna that would have changed the taxonomic composition. However, this composition is identical throughout the section. Therefore the climate must had been very stable at the scale of kyr, most probably considerably longer then 100 kyr. During the temperature and/or humid oscillations, the assemblage would have changed. Also it is necessary to consider that within habitat, the fossils come from near the water body, that is, from a humid area (although influence of dry air could not be excluded definitely). Also, there is no apparent indication of aridity of the Shar-Teg deposits and biota.

The age of Shar-Teg may also correspond to an interval of damaged ionosphere or ozone layer (possibly caused by the burst of gamma-ray in the milky way as shown by Thomas et al. (2005), which analogically may have caused extinction in the Ordovician), or an unusually long-lasting magnetic reversal resulting in the absence of the Van Allen radiation belts. This hypothesis appears to be the least probable because of an insufficient effect of a polarity change on biota evolution. A lack of association between the frequency of polarity change and the tempo of evolution cannot explain numerous changes during the Middle and Upper Jurassic which are shown by Gradstein et al. (2004) when insect evolutionary tempo was low; and few changes during the end of the Early Cretaceous to beginning of the Late Cretaceous. However an unusually long lasting (20 kyr and possibly more) low-intensity polarity period resulting in a period of low intensity of the geomagnetic field, may have affected the genome. (The last polarity change prior to the Jurassic/Cretaceous boundary [magnetozone M19r 445 ka (±5 kyr) (Houša et al. 1999, 2004)].)

Occurrences at the Jurassic/Cretaceous boundary were not as catastrophic as the events at the Permian/Triassic or even as the Triassic/Jurassic boundaries. Biota change at the J/K boundary was possibly caused by internal ecological reasons. Evidence is a long-lasting change, resulting in the absence of correlated boundary sections throughout the world and according diversification of the calcareous nannoplankton and stratification of the water in oceans, with consequent climate change in continents. This shift included a change of air-currents (e.g., the monsoonal climate replaced by more zonal paleoclimate (Weissert & Mohr 1996)), temperature decrease (Francis & Frakes 1993), global fall in sea level (Ruffel & Rawson 1994), start of the change to more arid climate (Allen 1981) and decrease in the C org/C carb burial possibly related to reorganization of the global climate system also resulting in decrease of reef growth (Weissert & Mohr 1996).

The biotically driven character of the changes is supported by the fact that although the Shar-Teg is the oldest assemblage of the modern type, its diversity is only moderate (Vršanský 2004). This phenomenon is less expressed at the family level (3000 specimens with 200 insect families (Gubin & Sinitza 1996; Ponomarenko 1998)) comparing with low diversity from the Lower Jurassic sediments of Germany (3821 specimens of about 120 families (Ansorge 2003, unpublished materials)) and high diversity from the Late Jurassic of Kazakhstan (18 000 specimens of at least 450 families (Panfilov 1968)).

Appearance of a new predator might cause destabilization of whole assemblages (e.g., newly evolved mantodeans or the like) even if their taxonomical composition would remain more or less stable. The radiation of mantids was possibly the result of a necessary control of the just-appeared plant-eaters attacking foliage.

The hypothesis of biotically driven changes seems to be the most promising since the faunal contact caused by the invasion of new predatory species, and ecosystem damage in the regions of the modern tropical forest also results in destabilization of morphological standard and increase of alleles creating deformities (see above).

Parasitoids may cause the abundant deformities on non-adapted insects of that time. The number of living insects influenced by parasitoids causing wing deformities contribute up to 4 % (Thompson 1986; Naranjo 2001). A higher ratio (up to 11 %) is reported only for lepidopteran *Ephestia kuehniella* parasitized by *Trichogramma brassicae* (Babendreier et al. 2003).

Nutrient deficiency also may cause wing deformities (Reddy & Chippendale 1972) in a frequency 17–27 % even if the population of insects is supported by antibiotic packages (Qureshi et al. 2004). The lack of free fatty acids (oleic, linoleic acids) may also cause wing deformities in insects, but this is not the case for the Shar-Teg since the absence of food in such long period would be hardly explainable.

Another possible agent might be bacterial, viral or protist infections which may cause wing deformities in bees (Fujiyuki et al. 2004; Chen et al. 2005) when attacking larvae. The induction of wing deformities by viruses (DWV — deformed wing virus) is also used for a Polymerase Chain Reaction detection (Tentcheva et al. 2004). Bacterial infection may also cause a production of toxic substances which may cause wing deformities preventing successful mating and reproduction (Naranjo & Prabhaker 2000). The same effect is known to be caused by a non-steroidal ecdysone agonist RH-5992 tebufenozide (Sundaram et al. 2002).

Protozoans such as *Trypanosoma rangeli* may regulate the whole populations of insects and the partition of wing deformities may reach up to 50 % as evidenced in hemipteran *Rhodnius domesticus* (Guarneri et al. 1997).

Wing deformities may also be caused by products of some plants such as azadirachtin contained in the neem tree, *Azadirachta indica* (Martinez & van Emden 2001). The Jurassic/Cretaceous boundary falls within the evolution of new plant taxa such as angiosperms, which possibly might have been able to produce such insecticides, but even in such case, their influence on predators seems unlikely.

Thus, the most probable hypothesis is the destabilization of the whole ecosystem, which might have been a result of the appearance of new taxa such as new foliage-eaters, social decompositors and predators (Vršanský 2002, 2004). As the dating of the Shar-Teg locality shows (Gubin & Sintza 1996), this appears to have occurred before the boundary.

The presence of abundant mutations near the boundary may explain the appearance of new taxa as a result of increased variability. Actually, the happenings at the Jurassic/Cretaceous boundary triggered a great success of dictyopterans. Social termites and mantids radiate immediately after the boundary, as well as the just appearing new families Blattellidae (relatives of the common synantrophic cockroach *Blattella germanica*), the Holocompsidae and the beetle-like Umenocoleidae. Additionally, advanced genera of the Mesozoic families Blattelidae and Caloblattinidae appear, while no archaic genera or families disappear from the fossil record at that time. More than this, a revolutionary change occurs in cockroaches — groups which lay ootheca radiate and replace those laying single eggs, which had been common in the Mesozoic. The age of the origination of the modern egg-eating midges is roughly estimated to the Late Jurassic–Early Cretaceous (unpublished observation), and thus their role in the selection of the ootheca producers could not be excluded.

It is notable that the Shar-Teg is probably the only Mesozoic locality where presumably nocturnal Caloblattinidae are absent. Nevertheless other nocturnal insects such as some neuropterans are common, which may indicate the environmental stress was not especially expressed during the night. In spite of the enhanced mutability and evolution and/or radiation of the modern groups, the Mesozoic groups of cockroaches show unusual stability and pass through the boundary without remarkable changes.

Additionally, a general coherence is worth mentioning: the evolutionary tempo of insects was significantly rising near the end of the Jurassic which is connected with the decreased extinction and higher diversification rates, as seen among wasps and flies (Dmitriev & Ponomarenko 2002; A.P. Rasnitsyn — personal communication); cockroaches, mantids and termites (Vršanský 2004). At least in the three latter groups, the evolutionary tempo at family level, was low after the Shar-Teg times. It appears that the saturation of niches (sensu Zherikhin & Rasnitsyn 1980; Zherikhin 1987; Rasnitsyn 1988) took place. The long, over 30-million-years lasting stability of ecosystems (until the paradoxical phase of ecosystem change during the Albian) was apparently caused by new control mechanisms, such as modern decompositors including social termites, predators, foliage consumers and others, which radiate during that time.

The normal, stable ecosystem lowers the evolutionary tempo of respective elements (Zherikhin 1978), thus keeping the stability and regular tempo of evolution of the whole ecosystem — possibly it regulates the number of available niches through the amount of energy available for use by competent organisms. It appears very probable that initially, the new control mechanisms destabilized ecosystems, in which case the evolutionary tempo of the respective elements, namely species, is uncontrolled according to Zherikhin (1987) and Rasnitsyn (1988). This caused population fluctuations and change of other factors, among which the most important was structural change of selective pressure (as it is recognized in recent activities of humans), allowing the accumulation of deformities. In the case that the mass deformities represent mutations, the Shar-Teg record might represent direct evidence for this comparatively rapid process at a scale of 100 kyr. The newly organized stable complexes were braking the evolution of respective taxa actively as shown by the standard composition of decompositors, with lower diversity.

It is a significant fact that the new Cretaceous ecosystems reached stability without using the elements most characteristic of the living ecosystems, namely true flowering plants and ants. Thus, they probably did not exist during that time, but precursors of true flowers are expected (Ren 1998). (The ecological role of angiosperm plants was growing up slowly during the Cretaceous, in contrast to their diversity (Dmitriev & Ponomarenko 2002) and the integration of the flowering plants-pollinating insects complexes caused the consequent changes of ecosystems at the Early/Late Cretaceous and Mesozoic/Cenozoic boundaries.)

The agent triggering change at the Jurassic/Cretaceous boundary, unlike changes at the K1/K2 and K/T boundaries, which were triggered by changes of the primary producers at the lower trophic levels causing destabilization of whole succession and trophic structures (Zherikhin 1978, 1987), might well be represented by rapidly evolving insects as shown by deformities.

The social decompositors were integrated into newly forming ecosystems, and radiated. In the case they were common in the ecosystems (termites are known from the Berriasian and common in the fossil record from the Hauterivian), they might have represented a major stabilizing agent, which actively returned the organic carbon into the ecosystems. Thus they might have also caused a sharp decrease in the Productivity/Biomass ratio, which is a main trend in the evolution of ecosystems according to Krassilov (1992). In the initial stages of their radiation, the change in the cycle of organic Carbon might have destabilized the primary producers especially in the early successive stages.

Control and thus a stabilized number of niches in the decomposition chain at the J/K boundary is indicated by considerably lower species diversity of cockroaches in ecosystems of the Cretaceous compared to the Middle and Late Jurassic. Nevertheless, it must be stressed that the role of termites in ecosystems, as we know it today, probably began only with the appearance of modern termite families during the Tertiary.

Structural changes in the decomposition chain are indicated also by dominance of beetle *Mesocinetes* sp. (Eucinetidae), which was a saprophagous forest inhabitant according to A.G. Ponomarenko (personal communication). This, supported by the radiation of modern predators indicate a raised primary production of ecosystems. The radiation at the same time of eusocial termites, predatory mantids and modern cockroaches — groups belonging to one lineage — is notable.

Altogether, the J/K boundary might be characterized as a preparation phase of the ecosystem change with comparatively high extinction and higher appearance ratios, which is supported by lack of short-living families at the Shar-Teg and absence of relics. The next phases might be characterized by true flowering plants, which were initially rather common; almost completely absent in the next, paradoxical phase, and common again from the dramatic phase (Rasnitsyn 1988).

The current observation support a gradual change at the J/K boundary, without indications of dramatic extinction at generic and higher levels. This indicates that the period of destabilization lasted well under 1 Myr.

## Conclusions

— Enhanced environmental stress during some periods such as during the boundary times might have caused the occurrence of mass mutations which significantly contribute to the variability of species. This might have resulted in the origin and/or the rapid evolution of higher taxa.

— New control mechanisms such as modern decompositors including the social ones, predators and others, temporarily destabilized and subsequently stabilized ecosystems near the J/K boundary. Accordingly, Laurasian ecosystems remained stable for at least 30 Ma, with identical composition of some of its elements.

— The Shar-Teg deposits near the J/K transition in Mongolia display mass insects deformities expressed as fusion of wing veins which most probably represent heritable mutations.

— The partition of the modified individuals in some groups reach 15–20 %. Their accumulation was allowed by a changed structure of selective pressure during the period of ecosystem destabilization.

— Deformed individuals are preserved in strata of slightly different age (scale 100 kyr), indicating a long-lasting environmental stress and biotic character of the changes. On the other hand, the low extinction rates at the generic and higher levels indicate that the period of destabilization lasted considerably less than 1 Myr.

— Similar deformities are also recorded in the Recent ecosystems undergoing elevated environmental stress indicating similarity of Recent changes across the food web in these habitats.

— Deformities of caddis-flies appear later fixed in taxa of the family rank, thus supporting the heritable character of the deformities and the significance of enhanced mutability during the events for the process of evolution.

— The earliest Cretaceous assemblages of Asia are characterized by the presence of flowering plants and some modern insects, while in other continents they are missing. The Shar-Teg, additionally characterized by the presence of mass mutations, is the oldest locality of the Cretaceous type.

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