

Insect recovery after the Permian/Triassic crisis

Dmitry E. SHCHERBAKOV¹

¹Paleontological Institute, Russian Academy of Sciences,
Profsoyuznaya 123, Moscow 117647, Russia.
E-mail: dshh@narod.ru

ABSTRACT

Three main stages of insect fauna development in the Triassic are outlined: Early Triassic survival ('post-Paleozoic'); Anisian–Carnian acme ('Triassic *sensu genuino*'); Carnian–Norian rise of the Late Mesozoic elements ('pre-Jurassic'). Rhaetian insect fauna is virtually indistinguishable from the Early Jurassic one ('quasi-Jurassic'). Changes in aquatic insect assemblages are specially considered.

KEY WORDS: Entomofauna. Fossil record. Triassic. 'New aquatics'.

INTRODUCTION

Dozens of fossil insect localities are now known in the Middle–Late Permian and Triassic of European Russia, Urals, Siberia (especially Kuznetsk and Tunguska basins), Kazakhstan, Kyrgyzstan and Mongolia. The succession of insect assemblages across the Permian/Triassic boundary known in this region is the most complete in the world.

Paleoclimatic reconstructions show some five zonal biomes in the Middle to Late Permian; entomofaunas were differentiated according to these climatic zones and showed high taxonomic turnover. Becoming locally extinct in the Middle Permian, at least some Paleozoic relict groups survived until terminal Permian in refugia with favourable climate, e.g. near the transition from semiarid to temperate zone in the Northern Hemisphere (Subangaria in broad sense), and coexisted there with the first members of some Mesozoic groups (appearing since the Middle Permian). About the Permian/Triassic boundary climatic zonality decreased (only three zonobiomes are reconstructed for the Triassic) and important changes took place in the insect assemblages (Shcherbakov 2000, 2008), analogous to those recorded in fossil floras (Looy *et al.* 2001): (i) shift of dominance to previously uncommon groups after the (near-)extinction of former dominants; (ii) appearance of 'new' groups that in some instances were also recorded at low latitudes in the Late Permian and probably represent long-range polarward migrants; (iii) enhanced survival of small-sized, non-specialized groups that may be mostly regarded as ecological generalists; (iv) enhanced survival of (semi)aquatic groups.

The Triassic period encompasses a transition from the Paleozoic biota to the typically Mesozoic one. It was the time when several insect orders and suborders that play a major role in modern ecosystems were established, such as the Diptera, Hymenoptera, Heteroptera, plus Adephaga and Polyphaga among Coleoptera. The development of the Triassic megafloora was subdivided into three stages by

Dobruskina (1982), and analogous stages may be proposed for entomofaunas.

The present account is partly based on the papers by Ponomarenko & Sukatsheva (1998, 2001) and the multiauthored book *History of Insects* (Rasnitsyn & Quicke 2002). Dynamics of the insect taxonomic diversity in the Permian and Triassic and composition of entomofaunas are considered in a recent paper (Shcherbakov 2008).

THREE MAIN STEPS IN TRIASSIC INSECT HISTORY

1. **Early Triassic** – 'Post-Paleozoic', analogous to the 'Post-Paleophytic' megafloreal stage (term introduced by Meyen 1972). Low diversity post-crisis assemblages consist mainly of survivors from Permian faunas, but differ from the latter in numerical composition: abundant are groups that were rare in earlier assemblages, whereas the former dominants are absent or uncommon. Few families endemic to the Triassic appear at this stage. These faunas are still rather similar to the Late Permian ones in taxonomic composition and therefore sometimes dated paleontologically as the end-Permian or are assigned to the P/T boundary beds.

The Early Triassic insect record is rather scarce: impoverished assemblages are known from Nedubrovo (lower Vokhma Formation, Induan; Lozovsky *et al.* 2001) at the Yug River, Tikhvinskoe (Rybinsk Formation, Lower Olenekian) at the Volga River and several other sites in European Russia, from several localities in intertrappean deposits of the Tunguska Basin, and from the upper Yaman-Uus Formation (Induan) of South Mongolia (Aristov 2005). They are usually dominated by protorthopterous family Chaulioiditidae (=Tomiidae). A larger collection (some 150 insects) was obtained from the basal Triassic (Maltsevo Group) of Babiy Kamen' ("Woman's Rock") at the Tom' River, Kemerovo Region (Kuznetsk Basin). This assem-

blage is not taxonomically diverse, being dominated by various beetles, subdominated by Chaulioditidae and Auchenorrhyncha and also containing Orthoptera (earliest Mesoedischidae; data on Orthoptera from Gorokhov 2005a, b), Geinitziidae (Protorthoptera), Blattodea, Ephemeroptera (Misthodotidae), Neuroptera (Archaeosmylidae: Ponomarenko & Shcherbakov 2004) and Mecoptera (indet.). The Auchenorrhyncha are represented by the Prosbolidae (last record of the family widespread in the Middle–Late Permian), Hylcellidae (first record of Cicadomorpha: Clypeata) and Scytinopteridae. The occurrence of cockroaches in this site is noteworthy as they are absent in the underlying Middle–Late Permian sequence (about ten localities) of the Kuznetsk Basin; these cockroaches are small-sized (like those from the earliest Triassic of European Russia and in contrast to large *Aissoblatta* Handlirsch and allies common in the Late Kazanian–Vyatkian of the same region). Beetles are often preserved in entirety, so it is possible to place them in the natural system (isolated elytra are classified into form families; Ponomarenko 2004). The Ademosynidae and Schizophoridae are less common, and more common groups are the Triaplidae (family endemic to the Triassic; first record of Hydradephaga and Haliploidea) and the extant Trachypacheidae (first Geadephaga: Caraboidea), Hydrophilidae, Byrrhidae and Elateroidea (first Polyphaga). Isolated elytra similar to the families listed above are also known from the terminal Permian, so some of these groups presumably originated before the Triassic.

Other important Early Triassic finds are the first record of orthopteran infraorder Acrididea (Locustavidae) and the latest records of Archescytinidae and Ignotalidae, all in intertrappean deposits of the Tunguska Basin.

The richest of the Early Triassic assemblages, Babi Kamen' and upper Yaman-Us, are Induan. A very poor assemblage is known from the Early Olenekian of Tikhvinskoe (schizophoroid elytra and fragments of cockroach and protorthopteran wings). The assemblage of Khey-Yagha, Polar Urals dated Late Olenekian–Anisian (Nyadeita Formation) is more diverse, containing various beetles (Tricoleidae, elytra of Schizophoroidea and/or Adephega and probably of Polyphaga), Auchenorrhyncha (Scytinopteridae) and cockroaches (Ponomarenko 2008).

2. Middle to early Late Triassic: the heyday of Triassic groups and appearance of many Meso-Cenozoic orders, suborders and superfamilies. The majority of well-known Triassic localities belong in this stage.

At the beginning of this stage stands the early Anisian Grès à Voltzia, Vosges, France with ca. 5300 insects collected (Papier *et al.* 2005; Sinitshenkova *et al.* 2005). This entomofauna contains the earliest known Diptera (but no Hymenoptera yet). The assemblage is numerically dominated by Blattodea, subdominated by diverse Coleoptera (which appear to be the most diverse), Ephemeroptera and Auchenorrhyncha and contains considerable number of Diptera and Protorthoptera (other orders are rather uncommon). The taxonomic composition of this fauna is very unevenly studied. As currently known, 20 families or

higher taxa show their earliest records in this fauna, including such important groups as the extant mayfly suborder Euplectoptera (Siphonuridae), orthopteran infraorders Tettigoniidea (Hagloedischiidae, Tuppellidae) and Gryllidea (Gryllavidae), aphids, true bugs, extant beetle family Cupedidae, peculiar Mesozoic scorpionfly family Pseudopolycentropodidae, extant crane fly family Limoniidae, earliest Ptychopteroidea (Nadpteridae), and dipteran suborder Brachycera. Regular finds of dipteran pupae and adult *Grauvogelia* Krzeminski *et al.* 1994 indicate that at least some of the Vosges dipterans were amphibiotic. Seven families are considered endemic to, and two others have their last records in the Voltzia sandstone, including one of the last finds of the Chaulioditidae, a family characteristic of the first half of Triassic (a probable later find occurs in the Middle Triassic of Guizhou, China; Aristov 2003).

Other Anisian insects are found in the Hawkesbury Sandstone at Brookvale and Ashfield Formation at St. Petersburg, Sydney (earliest Triassic homopteran family Curvicutitidae; Jell 2004) and several minor localities.

The next oldest is the Madygen Formation of southern Fergana, Kyrgyzstan with its more than twenty thousand insect specimens and greater than 500 species; this Ladinian–Carnian locality constitutes much of our knowledge of Triassic insects (Shcherbakov, this volume). Its richness in the first records (28), last records (16) and endemic families (12) is at least partly due to enormous number of specimens collected and the selective collecting of rarities in this king-size locality (Alekseev *et al.* 2001). The entomofauna includes 25 species of the earliest Hymenoptera, all belonging to the extant family Xyelidae (Rasnitsyn 1969), and several families of early Diptera (Shcherbakov *et al.* 1995). Other important first records are Triasolestidae (earliest members of Libellulina *sensu* Pritykina), Aeroplanidae (Phasmatodea), Tridactylidea (Dzhajlouts-hellidae), Haglidae, the stonefly family Siberioperlidae (common in Jurassic), earwigs of the extant suborder Forficulina (Protodiplateidae), Cocomorpha s.l. (Naibiidae), supposed weevils (Obrieniidae), Mesozoic caddisfly families (Necrotauliidae, Prorhacophilidae), and possibly also ochteroid littoral bugs, the scorpionfly family Orthophlebiidae and the lacewing families Osmylidae, Polystoechotidae and Osmylpsychopidae. Among the last records are the Titanoptera and Prochresmodidae.

The Carnian entomofaunas of South Africa (Molteno Formation; Anderson *et al.* 1998) and Australia (Mt. Crosby and Blackstone formations, Ipswich Coal Measures; Jell 2004) both have less than 1000 specimens, the latter being better studied. They look rather similar to the Madygen fauna, but are less diverse and somewhat more advanced (contain less Triassic endemics and more survivors into the post-Triassic). The most significant first finds are putative Neomegaloptera (Euchauliodidae) from Molteno and truly aquatic bugs of the family Triassocoridae and extant scorpionfly family Bittacidae from Ipswich. Eleven families endemic to the (Late Permian +) Triassic are last recorded from Ipswich.

3. **Remaining Late Triassic:** many characteristic Triassic taxa pass away, and several key groups of Jurassic and Cretaceous assemblages enter the record, including some amphibiotic families which dominate many post-Triassic entomofaunas – so-called ‘new aquatics’ (term coined by A.G. Ponomarenko).

The entomofauna of the Cow Branch Formation (Newark Supergroup; Solite Quarries, Virginia) with more than 3000 insects is the best known (Fraser & Grimaldi 1997). It is dated Late Carnian, but in several respects appears more advanced than two other insect faunas, Garzhovka, Ukraine (Protopivka Formation, Late Carnian–Early Norian) and Kendyrluk, East Kazakhstan (upper Tologoy Formation, Carnian–Norian or Norian–Rhaetian). The Kendyrluk assemblage, dominated by water bugs with swimming hind legs of the Triassic family Triassocoridae (known also from Ipswich), looks the least advanced. In the Garzhovka assemblage the first Gyrinoidea and isophlebioid dragonfly larvae of *Samarura* type, which is common in the Jurassic, are recorded. The Cow Branch fauna is the earliest assemblage yielding the Staphylinidae, abundant water bugs of extant families (Belostomatidae, Naucoridae and Notonectidae: Olsen *et al.* 1978: figs 3D,E), and possibly also Liadytidae. Both Kendyrluk and Cow Branch Formation contain the earliest Thysanoptera *s.str.* (Triassothripidae) and Dytiscoidea: Colymbotethidae (closely related to primitive Coptoclavidae) in Kendyrluk, *Mormolucoides* Hitchcock 1858 (Colymbotethidae or Coptoclavidae – see below) in the Cow Branch Formation.

If age estimates for the above three formations are correct, then a reason why the older fauna looks more advanced than the younger one may lie in the different paleolatitudinal positions of tropical Cow Branch (ca. 10°N) and extratropical Garzhovka (ca. 35°N) and Kendyrluk (ca. 55°N). The same may be true of the Early Anisian Grès à Voltzia (ca. 15°N) and Late Olenekian–Anisian Khey-Yagha (ca. 50°N), and for other cases. The low-latitude humid zone is considered the point of origin for many higher taxa that subsequently disperse polarwards (‘equatorial pump’ – Darlington 1957; ‘phytospreading’ – Meyen 1987), so faunal changes in different zonobiomes may advance earlier at low latitudes, especially at humid climates, and the boundaries between faunal stages may be diachronous (shown by oblique lines on Fig. 1).

The entomofauna of the English **Rhaetian** (Penarth Group and base of Lias Group; Jarzembowski 1999) is similar to that of overlying Jurassic beds, including the occurrence of several species known both from the Rhaetian and early Jurassic, *e.g.* the ensiferan *Bintoniella brodiei* Handlirsch 1939 (Whalley 1982) and cupedid *Omma liassicum* Crowson 1962 (belonging to the extant genus; Ponomarenko 2006a). This fauna is only ‘technically’ Triassic, as it cannot be differentiated from the earliest Jurassic fauna, and should be classified with other Jurassic faunas. Important novelties recorded in the English Rhaetian are isophlebioid Archithemistidae, Cicadoidea (represented by extant family Tettigarctidae), land bugs (Pachymeridiidae), Chironomoidea (Chironomidae), and undoubted

Orthophlebiidae. The earliest Grylloidea (Protogryllidae) from the Late Norian–Rhaetian Stormberg Series, South Africa, are represented by the same genus, *Archaeogrylloides* Haughton 1924, as in the Early Jurassic of England.

WATER INSECTS

Aquatic insect sub-assemblage is an important and indicative part of the fossil insect assemblage. A preliminary typology of Triassic aquatic assemblages was suggested by Sinitshenkova (2002), based mainly on numerical dominance of the fauna by mayfly and/or stonefly nymphs, larval and adult beetles, or aquatic bugs. True bugs, first recorded in Vosges, were originally littoral and only subsequently evolved into truly aquatic (since Ipswich) and terrestrial (since Rhaetian) forms, so the water bug abundance in the Triassic is time-dependent, in addition to being environment-dependent (in Jurassic–Cretaceous, abundance was highest in mineralized, oxygen-poor lakes). Therefore, we should probably pay more attention to the other aquatic insect groups, making a distinction between those groups which breathe dissolved oxygen via tracheal gills at the nymphal/larval stage (Ephemeroptera, Odonata, Plecoptera, Megaloptera, Trichoptera, some aquatic Coleoptera and Diptera) and those using atmospheric air (all Mesozoic aquatic Heteroptera, most aquatic Coleoptera, many aquatic Diptera). Aquatic beetles known from the Triassic include archostematan Schizophoroidea (they possessed elythro-thoracic interlocking device, ‘schiza’ to store the air under elytra, but were not actively swimming), adepagan Haliploidea (Triaplidae), Dytiscoidea

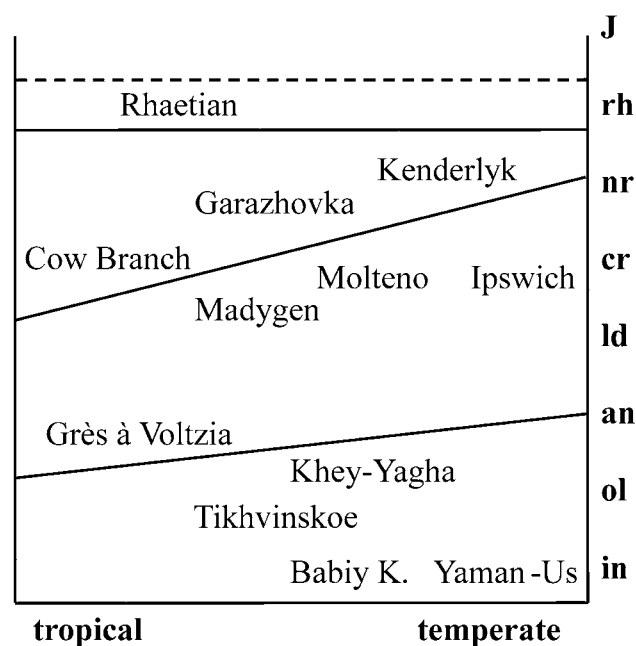


Figure 1. Three main stages of entomofauna development in the Triassic, with the faunas discussed in text. The boundaries between stages probably diachronous, the changes proceeding in advance at low latitudes, especially at humid climates.

(Colymbotethidae, Coptoclavidae, Liadytidae) and Gyri-noidea (*Triadogyrus* Ponomarenko 1977), and polyphagan Hydrophilidae. Dipterans with aquatic larvae recorded in the Triassic are Ptychopteroidea and Chironomidae, probably also Grauvogeliidae and some Limoniidae, and presumably some (if not all) others.

The earliest Triassic assemblage of Babiy Kamen' contains adult mayflies (Misthodotidae), adult water beetles (Schizophoridae, Triaplidae, Hydrophilidae), and numerous adult Chaulioditidae, which also possibly had amphibiotic nymphs.

The Anisian fauna of Grès à Voltzia, Vosges, dwelling in a deltaic environment (fluvial channels and temporary pools) with marine incursions (Briggs & Gall 1990), contains diverse mayfly nymphs and adults, rare adult Odonata, rare (littoral?) bugs, aquatic coleopteran and possibly megalopteran larvae, Schizophoridae, and aquatic Diptera (numerous undetermined pupae, probably also Grauvogeliidae).

The Ladinian–Carnian Madygen fauna contains diverse amphibiotic insects (most numerous of them Schizophoridae), but only as adults (only 2 aquatic nymphs per 20000 insects!). The paleoenvironment was probably an oxbow-lake with the water mineralized and low in oxygen, and *Riccia*-like hepatics forming floating mats; gill-breathing phyllo-pods of the order Kazacharthra known from the same formation possibly dwelled in seasonal ponds on a floodplain (Shcherbakov, this volume).

Late Triassic assemblages contain, along with stonefly nymphs, several 'new aquatics', some of them adapted to swimming with the use of rowing hind legs. Triassocoridae and dytiscoid Colymbotethidae are found in Kendyrluk (along with phyllo-pod Kazacharthra), isophlebioid odonatan larvae of *Samarura* type, megalopteran larvae, Triaplidae and Gyri-noidea in Garazhovka, and mayflies Mesonetiidae and Torephemeridae in the Varengayakha Formation of West Siberia (formerly considered Middle Triassic). The more advanced Triassic aquatic insect fauna of the Cow Branch Formation, in addition to Schizophoridae and *Mormolucooides*, includes probable Liadytidae, extant water bug families (Belostomatidae, Naucoridae, Notonectidae), and probably some aquatic Diptera (their presumed pupae were figured as "?phyllocarid" in Olsen *et al.* 1978: fig. 4A). The Newark Late Triassic lakes, interpreted as deep, chemically stratified basins with anoxic hypolimnion (Olsen *et al.* 1978), were similar to the large Jurassic–Early Cretaceous lakes as interpreted by Kalugina (1980) and Ponomarenko (1996).

Mormolucooides from the Newark Supergroup, regarded as megalopteran or coleopteran larva (see *e.g.* Handlirsch 1906–1908), was later considered to be a heterogeneous taxon, and some specimens assigned to it were interpreted (based mainly on earlier drawings) by Ponomarenko (1993, 1996) as dytiscoid larvae related to Coptoclavidae and Colymbotethidae. The *Mormolucooides* larvae are now recorded in both Triassic (Cow Branch Formation) and Early Jurassic part of the Newark Supergroup; in the Juras-

sic part they co-occur with elytra of the genus *Holcoptera* Handlirsch 1906 (Huber *et al.* 2003) and most probably represent the larvae of *Holcoptera*, that was interpreted as a coptoclavid near to *Coptoclavella* Ponomarenko 1980 (Ponomarenko *et al.* 1999).

In the English Rhaetian, Chironomidae join the list of 'new aquatics'.

The successive changes of aquatic insect assemblages in the Triassic were considered as demonstrating the massive parallel expansion of many terrestrial insect lineages into continental waters, in accordance with hypothesis on the non-aquatic origin of Pterygota accepted by many coauthors of *History of Insects* (Rasnitsyn & Quicke 2002). This colonization of fresh waters by Triassic insects is apparently overrated, because of the following arguments.

There are strong reasons to consider the tracheal gill-breathing aquatic immatures primitive for the Pterygota, Neoptera, and Holometabola (Omodeo *et al.* 1980; Kukulová-Peck 1983; Shcherbakov 1999). The fact that the earliest known Holometabola are caddisflies Protomeropidae (Late Carboniferous: Nel *et al.* 2007) agrees with this idea. The origin and early evolution of higher Coleoptera (Adephaga and Polyphaga), Diptera and Heteroptera were all intimately connected with aquatic environments (Ponomarenko 1977, Kalugina 1980, Shcherbakov & Popov 2002), taking place during the latest Permian–Early Triassic (so far as is known, beetles were the earliest to evolve this way and true bugs the latest). Only Heteroptera may doubtless be regarded secondarily aquatic, in a sense that their remote auchenorrhynchous predecessors were surely terrestrial; however, the Scytinopteroidea, directly ancestral to true bugs, show elythro-thoracic interlocking device analogous to the beetle 'schiza' and presumably lived on helophytes and were tolerant to submersion (Shcherbakov 2000). Already the Early Anisian entomofauna contains diverse gill-breathing immatures along with water beetles and aquatic true flies. Truly aquatic bugs and other groups with swimming adaptations appeared in the Late Triassic. The extreme rarity of aquatic immatures in some Triassic (*e.g.* Madygen) and most Permian insect assemblages is due to taphonomic bias and probably also some peculiarities of the ancient lakes, and there is no need to hypothesize terrestrial habit for the earliest dragonflies and caddisflies. Few Permian assemblages contain a considerable percentage of aquatic nymphs, *e.g.* Early Permian Elmo, Kansas or Middle Permian Kostovaty, Udmurtia (mayfly and stonefly nymphs constitute about 10% of total insects: Shcherbakov 2008).

CONCLUSIONS

Based on the fossil insect record available, three stages of entomofauna development in the Triassic can be discerned, analogous to those proposed for floras: (i) Early Triassic survival – low insect diversity and abundance for some 5 Myr; the faunas comprise mainly Permian groups, but in proportions unusual for the Permian ('post-Paleozoic'); (ii) Anisian–Carnian acme – highly diversi-

fied insect fauna rich in Triassic endemics and containing many Mesozoic and extant taxa ('Triassic *sensu genuino*'); (iii) Carnian–Norian rise – less diverse faunas enriched with Late Mesozoic dominants, especially with 'new aquatics' ('pre-Jurassic').

The boundaries between these faunal stages may be diachronous, if development of faunas proceeded in advance at low latitudes, especially at humid climates.

The English Rhaetian is indistinguishable in the terms of insect assemblage from the earliest Jurassic (including shared insect species), and should be considered an integral part of the Early Jurassic stage of entomofauna development ('quasi-Jurassic').

The impoverished Induan–Olenekian entomofaunas existed during a period of lycopsid dominance, following the massive dieback of gymnosperm vegetation and degradation of terrestrial ecosystems at lower latitudes; equatorial forests re-established only during the end-Olenekian (Looy *et al.* 1999). The early Anisian insect fauna is not yet as diverse as some of the best known Middle and Late Permian assemblages, does not contain Hymenoptera and apparently immediately follows the recovery of terrestrial ecosystems. Restoration of the fully diversified entomofauna by the later Middle Triassic is roughly synchronous to that of peat-forming plants and tropical coral reefs (end of the coal gap: Retallack *et al.* 1996). Virtual absence of xylomycetophagous beetles (Permocupedidae–Cupedidae lineage, Tricoleidae) in the terminal Permian and Early Triassic assemblages is associated with a decline of arboreal vegetation (Ponomarenko 2006b). The terminal Triassic insect fauna is indistinguishable from the earliest Jurassic one, confirming the idea that crucial ecosystem transformations on the land occurred ahead of those in the sea (Ponomarenko 2006b).

We must briefly comment on the paper by Bethoux *et al.* (2005) entitled "The Triassic radiation of the entomofauna". These authors write that "a gap of 15 Myr separates our Latest Permian record from the Earliest Triassic one" in those groups which they selected as models to investigate insect radiation after the Permian/Triassic extinction (Orthoptera and allies; Odonata), referring mostly to the faunas of the Permian Salagou Formation, Lodève Basin and the Middle Triassic Grès à Voltzia of Vosges, France. Their calculation seems strange: several well known terminal Permian entomofaunas (*e.g.* from Sydney and Karoo basins) are at most 7–8 Myr older than Grès à Voltzia (and the basal Triassic assemblage of Babiy Kamen' is about 5 Myr older). Such a statement may be (and immediately was – Bottjer & Gall 2005; Knoll *et al.* 2007: 305) misinterpreted as a 15 Myr gap in the documented history of all insects. There are many real gaps in the fossil record and no need to invent imaginary ones.

ACKNOWLEDGEMENTS

The author is grateful to Prof Alexander G. Ponomarenko (Paleontological Institute, Russian Academy of

Sciences (RAS), Moscow) for valuable discussion and help, to Dr Ed Jarzembowski (Maidstone Museum & Bentlif Art Gallery) and Dr André Nel (Muséum National d'Histoire Naturelle, Paris) for reviewing the paper, and Dr Sarah Martin (Monash University, Clayton) for improving the English of the manuscript. The study is supported by the Russian Foundation for Basic Research (project 07-04-01158) and the Presidium of RAS program "Biosphere origin and evolution".

REFERENCES

- ALEKSEEV, A.S., DMITRIEV, V.Y. & PONOMARENKO, A.G. 2001. Evolution of taxonomic diversity. Ecosystem transformations and the evolution of the biosphere, GEOS, Moscow, 5: 1-126 [in Russian].
- ANDERSON, J.M., ANDERSON, H.M. & CRUICKSHANK, A.R.I. 1998. Late Triassic ecosystems of the Molteno/Lower Elliot Biome of Southern Africa. *Palaeontology*, 41: 387-421.
- ARISTOV, D.S. 2003. Revision of the family Tomiidae (Insecta: Grylloblattida). *Paleontological Journal*, 37: 31-38.
- ARISTOV, D.S. 2005. New grylloblattids (Insecta: Grylloblattida) from the Triassic of Eastern Europe, Eastern Kazakhstan and Mongolia. *Paleontological Journal*, 39: 173-177.
- BÉTHOUX, O., PAPIER, F. & NEL, A. 2005. The Triassic radiation of the entomofauna. *Comptes rendus Palevol*, 4: 609-621.
- BOTTJER, D.J. & GALL, J.-C. 2005. The Triassic recovery, the dawn of the modern biota. *Comptes rendus Palevol*, 4: 385-393.
- BRIGGS, D.E.G. & GALL, J.-C. 1990. The continuum in soft-bodied biotas from transitional environments: a quantitative comparison of Triassic and Carboniferous Konservat-Lagerstätten. *Paleobiology*, 16: 204-218.
- DARLINGTON, P.J. Jr. 1957. *Zoogeography: The Geographical Distribution of Animals*. Chapman and Hall, London: xiv + 675.
- DOBRUSKINA, I.A. 1982. Triassic floras of Eurasia. *Transactions of Geological Institute of the USSR Academy of Sciences*, 365: 1-196 [in Russian; English translation: Springer, Wien, 1994].
- FRASER, N.C. & GRIMALDI, D.A. 1997. Who else lived in the Late Triassic? – The world of the early dinosaurs as illustrated by a fossil lagerstaette in Virginia. In: *Dinofest International: Proceedings of a Symposium held at Arizona State University*, WOLBERG, D.L., STUMP, E. & ROSENBERG, G. (eds), Academy of Natural Sciences, Philadelphia: 191-198.
- GOROCHOV [GOROKHOV], A.V. 2005a. Review of Triassic Orthoptera with descriptions of new and little known taxa: Part 1. *Paleontological Journal*, 39: 178-186.

- GOROCHOV, A.V. 2005b. Review of Triassic Orthoptera with descriptions of new and little known taxa: Part 2. *Paleontological Journal*, 39: 272-279.
- HANDLIRSCH A., 1906-1908. Die fossilen Insekten und die Phylogenie der rezenten Formen. Wilhelm Engelmann, Leipzig: 1430 pp.
- HUBER, P., McDONALD, N.G., OLSEN, P.E. & ZIDEK, J. 2003. Early Jurassic insects from the Newark Supergroup, northeastern North United States. In: The great rift valleys of Pangea in eastern North America, v. 1, Tectonics, structure, and volcanism of supercontinent breakup, LeTOURNEAU, P.M. & OLSEN, P.E. (eds), Columbia University Press, New York: 206-233.
- JARZEMBOWSKI, E.A. 1999. Arthropods 2: Insects. In: Fossils of the Rhaetian Penarth Group, SWIFT, A. & MARTILL, D.M. (eds), Palaeontological Association, London: 149-160.
- JELL, P.A. 2004. The fossil insects of Australia. *Memoirs of the Queensland Museum*, 50(1): 1-124.
- KALUGINA, N.S. 1980. Insects in freshwater ecosystems of the past. In: Historical development of the class Insecta, ROHDENDORF, B.B. & RASNITSYN, A.P. (eds), Transactions of Paleontological Institute of the USSR Academy of Sciences, 175: 224-240 [in Russian].
- KNOLL, A.H., BAMBACH, R.K., PAYNE, J.L., PRUSS, S. & FISCHER, W.W. 2007. Paleophysiology and end-Permian mass extinction. *Earth and Planetary Science Letters*, 256: 295-313.
- KUKALOVÁ-PECK, J. 1983. Origin of the insect wing and wing articulation from the arthropodan leg. *Canadian Journal of Zoology*, 61: 1618-1669.
- LOOY, C.V., BRUGMAN, W.A., DILCHER, D.L. & VISSCHER, H. 1999. The delayed resurgence of equatorial forests after the Permian–Triassic ecological crisis. *Proceedings of the National Academy of Sciences*, 96: 13857-13862.
- LOOY, C.V., TWITCHETT, R.J., DILCHER, D.L., VAN-KONIJNENBURG-VAN CITTERT, J.H.A. & VISSCHER, H. 2001. Life in the end-Permian dead zone. *Proceedings of the National Academy of Sciences*, 98: 7879-7883.
- LOZOVSKY, V.R., KRASSILOV, V.A., AFONIN, S.A., PONOMARENKO, A.G., SHCHERBAKOV, D.E., ARISTOV, D.S., YAROSHENKO, O.P., KUKHTINOV, D.A., BUROV, B.V., BUSLOVICH, A.L. & MORKOVIN, I.V. 2001. On a new member of Vokhma Formation, Lower Triassic of Moscow Region. *Bulletin of Regional interdepartmental stratigraphic commission on central and southern Russian Platform*, 3: 151-163 [in Russian].
- MEYEN, S.V. 1972. Main problems of paleofloristics of the Carboniferous and Permian. *Results of science and technology, Ser. Stratigraphy, Paleontology*, 3: 94-107 [in Russian].
- MEYEN, S.V. 1987. *Fundamentals of Palaeobotany*. Chapman and Hall, London: 432 pp.
- NEL, A., ROQUES, P., NEL, P., PROKOP, J. & STEYER, J.S. 2007. The earliest holometabolous insect from the Carboniferous: a “crucial” innovation with delayed success (Insecta Protomeropina Protomeropidae). *Annales de la Société Entomologique de France (N.S.)*, 43 (3): 349-355.
- OLSEN, P.E., REMINGTON, C.L., CORNET, B. & THOMSON, K.S. 1978. Cyclic change in Late Triassic lacustrine communities. *Science*, 201: 729-733.
- OLSEN, P.E., MCDONALD, N.G., HUBER, P. & CORNET, B. 1992. Stratigraphy and paleoecology of the Deerfield rift basin (Triassic-Jurassic, Newark Supergroup), Massachusetts. In: *Guidebook for Field Trips in the Connecticut Valley Region of Massachusetts and Adjacent States (vol. 2)*. New England Intercollegiate Geological Conference, 84th Annual Meeting, Contribution no. 66, ROBINSON, P. & BRADY, J.B. (eds), University of Massachusetts, Amherst, Massachusetts: 488-535.
- OMODEO, P., MINELLI, A. & BACETTI, B. 1980. On the phylogeny of pterygote insects. *Bolletino di Zoologia*, 47 (suppl.): 49-63.
- PAPIER, F., NEL, A., GRAUVOGEL-STAMM, L. & GALL, J.-C. 2005. La diversité des Coleoptera (Insecta) du Trias dans le nord-est de la France. *Geodiversitas*, 27: 181-199.
- PONOMARENKO, A.G. 1977. Suborder Adepfaga. In: *Mesozoic Coleoptera*. ARNOLDI, L.V., ZHERIKHIN, V.V., NIKRITIN, L.M. & PONOMARENKO, A.G. Transactions of Paleontological Institute of the USSR Academy of Sciences, 161: 17-96 [in Russian, English translation: Oxonian, New Dehli, 1991].
- PONOMARENKO, A.G. 1993. Two new species of Mesozoic beetles from Asia. *Paleontological Journal*, 27(1A): 182-191.
- PONOMARENKO, A.G. 1996. Evolution of continental aquatic ecosystems. *Paleontological Journal*, 30: 705-709.
- PONOMARENKO, A.G. 2004. Beetles (Insecta, Coleoptera) of the Late Permian and Early Triassic. *Paleontological Journal*, 38 (Suppl. 2): S185-S196.
- PONOMARENKO, A.G. 2006a. On the types of Mesozoic archostematan beetles (Insecta, Coleoptera, Archostemata) in the Natural History Museum, London. *Paleontological Journal*, 40: 90-99.
- PONOMARENKO, A.G. 2006b. Changes in terrestrial biota before the Permian–Triassic ecological crisis. *Paleontological Journal*, 40 (Suppl. 4): 468-474.
- PONOMARENKO, A.G. 2008. New Triassic beetles (Coleoptera) from the northern European Russia. *Paleontological Journal*, 42: 600-606.
- PONOMARENKO, A.G., CORAM, R. & JARZEMBOWSKI, E.A. 1999. Fossil beetles (Insecta: Coleop-

- tera) from the Purbeck limestone group of Dorset – a preliminary report. *Dorset Proceedings*, 121: 107-112.
- PONOMARENKO, A.G. & SHCHERBAKOV, D.E. 2004. New lacewings (Neuroptera) from the terminal Permian and basal Triassic of Siberia. *Paleontological Journal*, 38 (Suppl. 2): S197-S203.
- PONOMARENKO, A.G. & SUKATSHEVA, I.D. 1998. Insects. In: Permian-Triassic boundary in the continental series of East Europe, LOZOVSKY, V.R. & ESAULOVA, N.K. (eds), GEOS, Moscow: 96-106 [in Russian].
- PONOMARENKO, A.G. & SUKATSHEVA, I.D. 2001. Insects of the terminal Triassic and basal Jurassic. Ecosystem transformations and the evolution of the biosphere, GEOS, Moscow, 5: 97-107 [in Russian].
- RASNITSYN, A.P. 1969. Origin and evolution of lower Hymenoptera. *Transactions of Paleontological Institute of the USSR Academy of Sciences*, 123: 1-196 [in Russian; English translation: Amerind, New Dehli, 1979].
- RASNITSYN, A.P. & QUICKE, D.L.J. (eds). *History of Insects*. 2002. Kluwer, Dordrecht: 517 pp.
- RETALLACK, G.J., VEEVERS, J.J. & MORANTE, R. 1996. Global early Triassic coal gap between Late Permian extinction and Middle Triassic recovery of peat-forming plants. *Bulletin of the Geological Society of America*, 108: 195-207.
- SHCHERBAKOV, D.E. 1999. Controversies over the insect origin revisited. *Proceedings of the 1st International Palaeoentomological Conference*, Moscow, 1998. AMBA projects, Bratislava: 141-148.
- SHCHERBAKOV, D.E. 2000. Permian faunas of Homoptera (Hemiptera) in relation to phytogeography and the Permo-Triassic crisis. *Paleontological Journal*, 34 (Suppl. 3): S251-S267.
- SHCHERBAKOV, D.E. 2008. On Permian and Triassic insect faunas in relation to biogeography and the Permian-Triassic crisis. *Paleontological Journal*, 42: 15-31.
- SHCHERBAKOV, D.E., LUKASHEVICH, E.D. & BLAGODEROV, V.A. 1995. Triassic Diptera and initial radiation of the order. *International Journal of Dipterological Research*, 6: 75-115.
- SHCHERBAKOV, D.E. & POPOV, Y.A. 2002. Order Hemiptera Linné, 1758. In: *History of Insects*, RASNITSYN, A.P. & QUICKE, D.L.J. (eds), Kluwer, Dordrecht: 143-157.
- SINITSHENKOVA, N.D. 2002. Ecological history of the aquatic insects. In: *History of Insects*, RASNITSYN, A.P. & QUICKE, D.L.J. (eds), Kluwer, Dordrecht: 388-417.
- SINITSHENKOVA, N.D., MARCHAL-PAPIER, F., GRAUVOGEL-STAMM, L. & GALL, J.-C. 2005. The Ephemeroidea (Insecta) from the Grès à Voltzia (early Middle Triassic) of the Vosges (NE France). *Paläontologische Zeitschrift*, 79: 377-397.
- WHALLEY, P.E.S. 1982. *Bintoniella brodiei* Handlirsch (Orthoptera) from the Lower Lias of the English Channel, with a review of British bintonellid fossils. *Bulletin of the British Museum of natural History (Geology)*, 36: 143-149.

Received: 5th March 2007

Accepted: 26th January 2008