

Galloisiana olgae sp. nov. (Grylloblattodea: Grylloblattidae) and the Paleobiology of a Relict Order of Insects

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ABSTRACT An extant species of the relict insect order Grylloblattodea is described from the Ussuri River Basin of southeastern Russia. This species, *Galloisiana olgae*, is a member of the family Grylloblattidae that probably originated as a lineage during the mid-Cenozoic and experienced subsequent range constriction associated with Pleistocene glaciation. The Grylloblattodea have a richer fossil history in warm-temperate habitats during the Late Paleozoic than the four confamilial genera of today would suggest. These modern taxa represent a specialized Cenozoic lineage that adapted to cool-temperate habitats in northwestern North America and northeastern Asia, and parallel other similar distributions of seed plants and insects.

KEY WORDS *Galloisiana olgae*, Grylloblattodea, rock crawlers, new species, paleobiology, Ussuri River Basin

THE GRYLLOBLATTIDS OR “rock-crawlers” are the least diverse of modern insect orders, consisting of 26 species, including a new species described below. All of the known extant species, which belong to the family Grylloblattidae, can be considered “living fossils” with presently relict distributions. The single extant family can be contrasted with >44 families described from the fossil record, which extend to the Late Carboniferous (Storozhenko 1992, 1997). Grylloblattodeans occupied diverse habitats during the Paleozoic and Mesozoic but currently are restricted to several specialized populations in northern, cool-temperate regions. The newly described species bears some of the most primitive features currently within the order and survives as a relict lineage from the mid-Cenozoic Turgai Forest of northern Eurasia.

Modern grylloblattids are wingless insects that live on and in soil, in caves, and beneath stones and in crevices of mountainous regions. They are principally carrion feeders on other insects though they will consume plant material (Pritchard and Scholefield 1978). They are extremely cryophilic, having a temperature optimum as low as 0°C (Henson 1957, Edwards 1982) and are negatively phototrophic and nocturnal when active (Rentz 1982). The order contains four extant genera, all occurring poleward of ≈35° latitude in cool-temperate areas of the Northern Hemisphere

(Fig. 1). Although living species are wingless, fossil representatives are fully winged and capable of flight (Rasnitsyn 1980). The correlated loss of wings, a subterranean life, and adaptation to cold temperature is a departure from the major evolutionary trend in Grylloblattodea that was established during the Mesozoic in warmer environments. Mesozoic species ancestral to the modern taxa were probably similar to *Grylloblattina*, the representative harboring the greatest number of primitive features, and a taxon that inhabits a mountainous region of the Khakaskaya Oblast in south-central Siberia (Fig. 1). *Galloisiana* also lives in old-growth, cool-temperate forest, in the Sikhote-Alin Mountains in the Ussuri River Basin, which also supports some plant species that are relicts of the mid-Cenozoic Turgai Forest. It was this locality in which the new species *Galloisiana olgae* sp. nov. was found, representing the northernmost occurrence of the order in the Far East of Russia. The Ussuri River Basin encompasses the greatest species-level diversity of this order and is the only region in which more than one genus of this order has been found.

Galloisiana olgae Vrsansky & Storozhenko, new species (Figs. 2 a–f and 3 b–e)

Material Examined. HOLOTYPE: female: Russia, Primorskii Region, Olga Mts., the basin of Vasilkovka River, 19.VIII.1997; collected by Vrsansky and Ihringova; repository in Zoological Institute, St. Petersburg.

Paratypes. Two adult females, 16–21.VIII.1997; immature males and females from the same locality not collected.

Adult (Female). Medium-sized for genus; dorsal body covered with numerous short hairs. Head broader than pronotum. Eyes 2.2–2.4 times longer than

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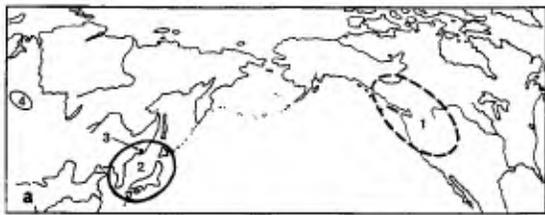


Fig. 1. Contemporary distribution of Grylloblattida. 1 *Grylloblatta* (11 species), 2 *Galloisiana* (12 species), 3 *Grylloblattina* (one species), 4 *Grylloblattella* (2 species).

wide, well pigmented. Parietal suture reaching eyes; frontal and clypeal sutures well differentiated. Antennae with 37–38 segments; third segment \approx 3 times longer than second. Pronotum as long as wide, with broadly rounded posterior margin. Cervical sclerite with 7–8 setae (macrotrichiae) on external margin. Basisternum oviform. Legs long; femur ratios (length divided by width) as follows: fore femur 2.8 times, hind femur 4.3 times; tarsal pulvilli relatively short. Hind margin of I tergite with 4 (2+2) setae, II–V tergites with 8 (4+4), VI with 10 (5+5), VII–IX with 6 (3+3); anterolateral part of II–VII tergites with 1+1 setae. Sternites with two regular rows of setae. Cerci 9-segmented (including weakly separated first and second segments). Ovipositor reaching fifth segment of cerci.

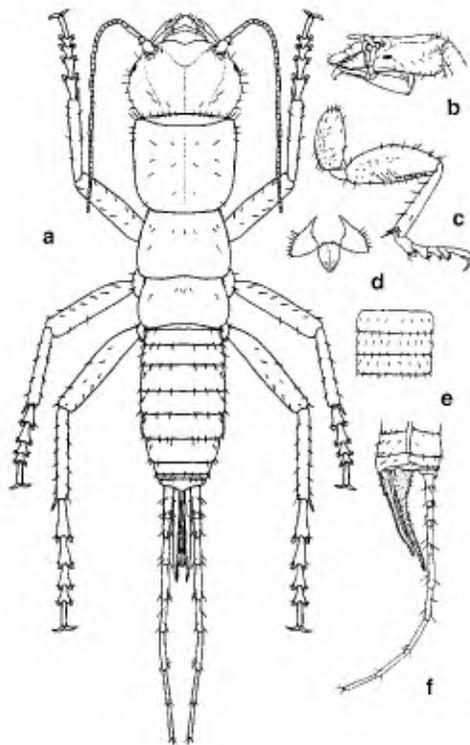


Fig. 2. (a) *Galloisiana olgae* sp. nov., female, (b) head, (c) fore leg, (d) cervical sclerites and basisternum, (e) 4–6 sternites, (f) apex of abdomen, lateral view.

Body brown, legs and ventral surface of abdomen light brown, ovipositor brown.

Body Dimensions (Holotype). Length: body 17.2 mm; head 4.5 mm; pronotum 3.6 mm; fore femur 3.7 mm; hind femur 4.7 mm; cerci 9.3 mm; ovipositor 3.7 mm. Width: head 4.0 mm; pronotum 3.6 mm.

Adult (male): Unknown. Immature male typically similar to female, including well pigmented eyes and number and placement of setae on body, but easily distinguished by structure of abdominal apex.

Comparison. This new species is closely related to *Galloisiana ussuriensis* Storozhenko, 1988 from Russia, *G. sofiae* Szeptycki, 1997 from North Korea, and *G. nipponensis* (Caudell and King 1924) from Japan. *G. olgae* sp. nov. is distinguished from the first two species by the number of tergal setae and by presence of two regular rows of setae on sternites. *G. nipponensis* differs from the new species by its elongated pronotum and shorter ovipositor.

Etymology. Found in Olginskij Chrebet, near the village of Olga, but named in the honor of Taiga goddess Olga, an inspiration to S.Y.S. for many years.

Biology and Biogeography. In addition to reduced eyes, the sensorial apparatus of grylloblattids is highly specialized. These features are associated with a highly localized, soil-based, and often subterranean existence. Thirteen distinct types of sensilla have been observed in modern grylloblattids (McIver and Sutcliffe 1982). The most noticeable are ocular setae, which serve as tactile sensors. Unlike all other species, *G. olgae* has heavily pigmented eyes from its earliest instar, which may indicate that this taxon is less subterranean than its congeners. Other externally evident microstructures of *G. olgae*, with an exception of the distribution of sensilla, are identical to those of *G. nipponensis* of Japan, indicating a close relationship between these species. Five populations of *G. olgae* have been identified in the Ussuri River region, all occupying banks of the Vasilkovka River. Each of these populations is distributed along a 50- to 150-m swath paralleling both river banks; each contains minimally several hundred individuals. The entire geographic range of the species is small, \approx 8 km². Typically, this species inhabits wet soil and can be found under rocks covered with moss. The annual average temperature of this habitat is under 8°C, and humidities approach 100% (unpublished data; also see Namkung 1982). The habitat of *G. olgae* contains vegetation that is considerably denser from that occupied by other grylloblattodean species (Fig. 2a). Notably, *G. olgae* always is associated with two species of angiosperms—one phylogenetically basal and the other advanced—namely, the magnoliid dicot *Schisandra sinensis* (Illiciales: Schisandraceae) and asterid dicot *Eleutherococcus senticosus* (Apiales: Apiaceae) (Plunkett et al. 1997, Qiu et al. 1999).

A relictual distributional pattern of closely related genera in northwestern North America and northeastern Asia typifies members of the Grylloblattidae, but also characterizes the distribution of many insects (Linsley 1963) and seed plant taxa, including species of *Metasquoia* (Cupressaceae), *Ginkgo* (Gink-

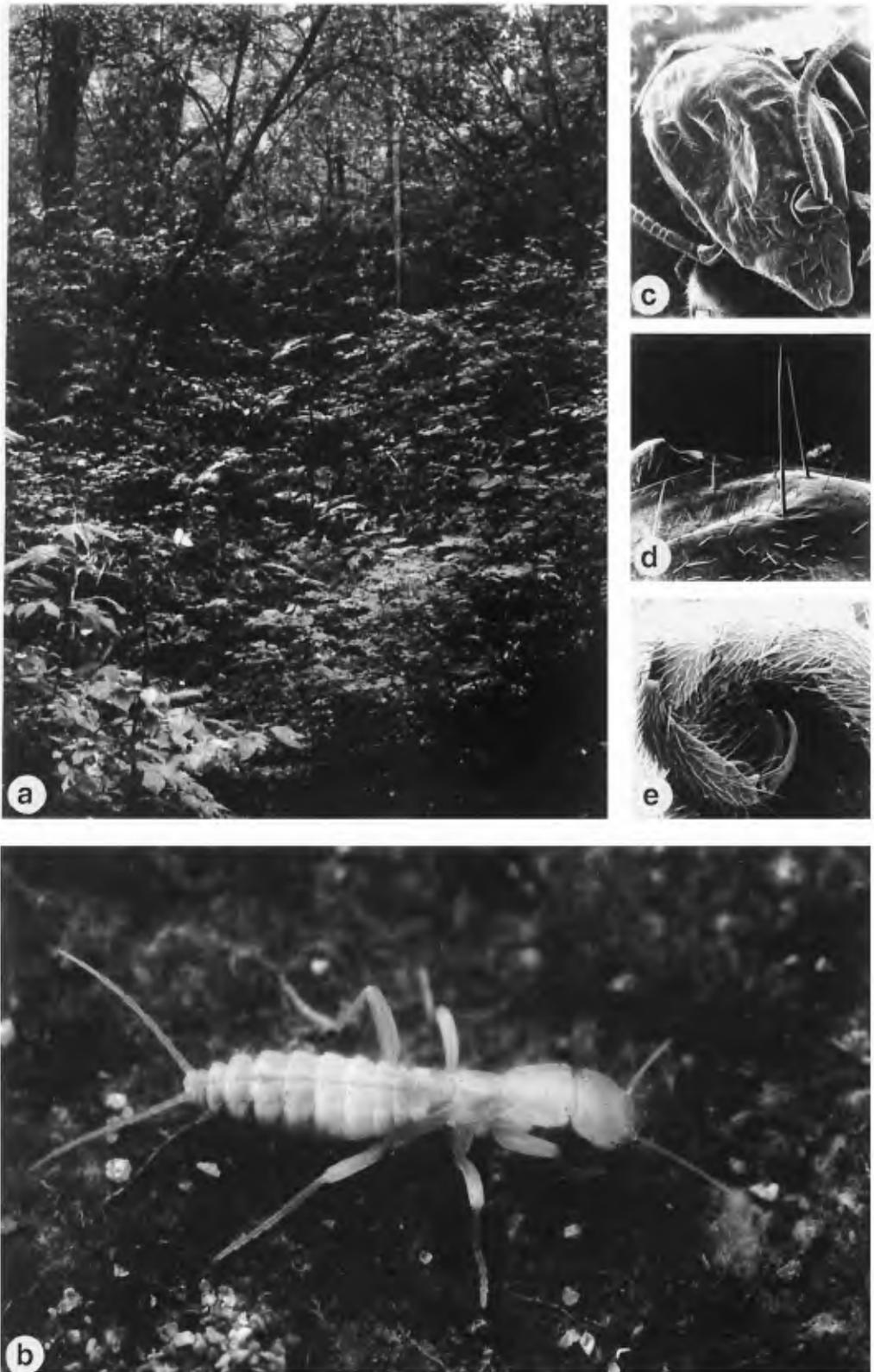


Fig. 3. *Galloisiana olgae* sp. nov. (a) habitat, (b) sixth immature stage, (c) head of second immature, (d) ocular seta, large and middle macrotrichia and microtrichia, (e) tarsus.

goaceae), *Cercidiphyllum* (Cercidiphyllaceae), and many angiosperms (Manchester 1999). The only exception is that the North American plant occurrences are extinct and occur commonly as fossils of Pacific Northwest floras, whereas the grylloblattids have survived to the present day in both regions. An additional, more intriguing, biogeographic parallel is the distribution of the wingless woodroach *Cryptoercus relictus* Bey-Bienko (Blattodea: Cryptoceridae), which inhabits rotting logs and occurs in the same general habitat as the Grylloblattidae. *Cryptoercus* probably represents a Cenozoic lineage of cockroaches that harbors wood-digesting intestinal symbionts (Nalepa et al. 1997, Nalepa and Bandi 1999), although this interpretation has been contested (Grandcolas 1999). Populations of *C. relictus* have been documented in the Ussuri Region near Slavyanka and Vladivostok (Bei-Benko 1935, 1950), and apparently its congeners, including *C. punctulatus* of the southern Appalachian Mountains, *C. evelandii* of the Pacific Northwest and *C. primarius* of Sichuan Province in China, are relictual populations confined to mountainous regions (Mamaev 1973, Asahina 1991, Nalepa et al. 1997). Nevertheless, new species have been observed in South Korea, North Korea, and in Yunnan Province of China (P.V. Vidlicka, and S.Y.S., unpublished data). Grylloblattodeans, like *Cryptoercus*, possess an elevated number of distinct species in this region, but the co-occurrence of two grylloblattodean genera that are restricted to southeastern Russia, the adjacent Korean Peninsula, and northern Japan, supports the hypothesis that this region was the center of origin for the extant genera.

Discussion

Because of the close taxonomic relationship between *G. olgae* and *G. nipponensis*, species similar to *G. olgae* presumably inhabited Japan during the mid-Cenozoic, when modern genera of East Asian Grylloblattidae originated. Their subsequent evolution in Japan and Korea reflects isolation and adaptation to a life primarily in caves (Nagashima et al. 1982, Namkung 1982). Undoubtedly, additional speciation took place in northeastern Asia during the Pleistocene, when species such as *G. olgae* presumably originated, as well as other related species in Japan, North Korea, and (sympatrically?) in the Ussuri River region. The distinctions among these species are morphologically subtle and involve differences of *G. olgae* from *G. ussuriensis*, *G. nipponensis* and *G. sofiae* that are based variously on chaetotaxy, ovipositor length, and pronotal size. A major influence in grylloblattid evolution was the ecological partitioning of their habitats, which in the case of the Russian taxa, probably was associated with renewed volcanic activity from the Sikhote-Alin Mountains, during the mid-Cenozoic (Bersenev and Vasiliev 1969). Later, during the Pleistocene or perhaps earlier in the Pliocene, some taxa became adapted to conditions at the edges of glaciers, of which modern species of *Grylloblatta* in northwestern North America are an example. These species

evidently migrated from refugia south of receding Cordilleran and Keewatin ice sheets during the latest Pleistocene, reaching their current distribution in the Holocene, where there has been subspecific differentiation (Kamp 1979). Speciation within the Grylloblattodea is a rare example of how a taxon can adapt to extreme conditions, given changing paleoenvironmental conditions and perhaps given competitive pressure by more advanced groups.

The order Grylloblattodea is believed to be ancestral, perhaps as a stem group, to several insect orders, including the Dermaptera, Plecoptera, and extinct Protelytroptera (Walker 1937; Rasnitsyn 1976, 1980; Rentz 1982; Storozhenko 1998). Nevertheless, the historical distribution of the order Grylloblattodea is enigmatic. During the Late Carboniferous, the group was present as two rare families, Protoperlidae and Daldubidae, and occurred in tropical to temperate Euramerican and Gondwanan localities (Storozhenko 1996a). Representatives from as many as 30 families are known from many fossil deposits of the Permian, albeit at the beginning of the Permian Period grylloblattids are absent, when the climate became more xeric and cooler, particularly for the Southern Hemisphere. Although largely based on negative evidence, this indicates that the group did not tolerate the cooler climates at that time. During the later Permian, the group was abundant and diverse (Storozhenko 1991, 1992); in several Permian sites the order comprises 30–50% of all insects. In particular, one member of the Grylloblattodea, *Sojanidelia florea* Rasnitsyn (Idelidae) from the mid-Permian Cherkada locality of the central Ural Mountains, consumed pollen of *Lunatisporites*, *Protohaploxypinus*, and two species of *Vittatina* (Rasnitsyn and Krassilov 1996, Krassilov and Rasnitsyn 1999). These pollen genera have been identified with conifer, glossopterid, peltasperm, and probably gnephtophyte seed plants (Clement-Westerhof 1974, Travers 1988, Zavada 1991, Balme 1995). From the same deposit, another grylloblattodean, *Tillyardembia antennaeplana* Zalesky (Tillyardemiidae), contained gut pollen of *Cladaitina* (Krassilov et al. 2000), whose source was the conifer-like male cones of ruffloriacean cordaites (Meyen 1987, Taylor and Taylor 1993). A third species, *Tschekardaenigma pollinivorum* Rasnitsyn, contained gut pollen similar to *Protohaploxypinus* (Rasnitsyn and Krassilov 1996). These three grylloblattodean taxa were representatives of a worldwide Late Paleozoic assemblage of spore- and pollen consuming insects (Labandeira 1998) that occupied the paleocontinents of Euramerica and Angara (the latter currently approximating Siberia), and indicate that there has been a dramatic dietary shift between Permian and recent members of the order (Krassilov and Rasnitsyn 1999). After a hiatus during the earlier Triassic, the fossil record of the Grylloblattodea resumes with the presence of 11 families in Middle and Upper Triassic deposits (Storozhenko 1996b), of which the Madygen locality of Kirghizistan is most notable (Storozhenko 1991, 1994). Successively younger occurrences are known from the Lower Jurassic localities at Soguty in Kirghizistan (Storozhenko

1991), Braunschweig in Germany (Storozhenko 1989), and the Upper Jurassic localities of Khotuiny-Khotgor in Mongolia (Storozhenko 1989) and Karatau in Kazakhstan (Rasnitsyn 1976, Doludenko et al. 1990), which contain rare material representing five families. From Lower Cretaceous deposits, particularly Baissa in the Transbaikalian region of Russia, three rare species from three families are known (Storozhenko 1989). The fossil record of the Grylloblattodea is absent from the mid-Cretaceous to the present. Apparently the extant taxa are a relatively late, specialized lineage adapted to cryophilic conditions where possibly competition with other ecologically equivalent groups was minimal.

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References Cited

- Alfonin, S.A. 2000. Pollen grains of the genus *Cladaitina* extracted from the gut of the Early Permian insect *Tillyardenbia* (Grylloblattida). *Paleontol. J.* 34: 575–579.
- Asahina, S. 1991. Notes on two small collections of the Blattaria from China and Korea. *Akitsu* 121: 1–5.
- Balme, B. E. 1995. Fossil in situ spores and pollen grains—an annotated catalog. *Rev. Palaeobot. Palynol.* 87: 81–323.
- Bei-Benko, G. 1935. Description of six new species of Palaeartic Blattodea. *Konowia* 14: 117–134.
- Bei-Benko, G. 1950. Blattodea, pp. 332–336. *In* Faune de l'URSS, New Series 20. USSR Academy of Sciences, Leningrad [in Russian].
- Bersenev, I. I., and B. I. Vasiliev. 1969. Late Cretaceous and Cenozoic structures, pp. 548–589. *In* I. I. Bersenev [ed.], Geology of the USSR, vol 32. Maritime Province, Part 1. Geological description, Nedra, Moscow [in Russian].
- Caudell, A. N., and J. L. King. 1924. A new genus and species of the notopterous family Grylloblattidae from Japan. *Proc. Entomol. Soc. Wash.* 26: 52–60.
- Clement-Westerhof, J. A. 1974. In situ pollen from gymnospermous cone of the Upper Permian of the Italian Alps—a preliminary account. *Rev. Palaeobot. Palynol.* 17: 65–73.
- Doludenko, M. P., G. V. Samulina, and A. G. Ponomarenko. 1990. Regional geologic structure and unique Late Jurassic occurrences of fauna and flora from Aulie (Karatau, Jurassic of Kazakhstan). USSR Academy of Sciences, Moscow.
- Edwards, J. S. 1982. Habitat, behaviour and neurobiology of an American grylloblattid, pp. 19–28. *In* H. Ando [ed.], Biology of the Notoptera. Kashiyo-Insatsu, Nagano, Japan.
- Grandcolas, P. 1999. Systematics, endosymbiosis, and biogeography of *Cryptocercus clevelandi* and *C. punctulatus* (Blattaria: Polyphagidae) from North America: a phylogenetic perspective. *Ann. Entomol. Soc. Am.* 92: 285–291.
- Henson, W. R. 1957. Temperature preference of *Grylloblatta campodeiformis* (Walker). *Nature (Lond.)* 179: 637.
- Kamp, J. W. 1979. Taxonomy, distribution, and zoogeographic evolution of *Grylloblatta* in Canada (Insecta: Notoptera). *Can. Entomol.* 111: 27–38.
- Krassilov, V. A., and A. P. Rasnitsyn. 1999. Plant remains from the guts of fossil insects: evolutionary and paleoecological inferences, pp. 65–72. Proceedings of the First Palaeontological Conference, Moscow, 1998: AMBA Projects International, Bratislava. Paleontological Institute of the Russian Academy of Sciences, Moscow.
- Labandeira, C. C. 1998. How old is the flower and the fly? *Science* 280: 57–59.
- Linsley, E. G. 1963. Bering Arc relationships of Cerambycidae and their host plants, pp. 159–178. *In* J. L. Gressitt [ed.], Pacific Basin biogeography. Bishop Museum Press, Honolulu, HI.
- Mamaev, B. M. 1973. Ecology of the relict cockroach (*Cryptocercus relictus*). *Ekologiya* 4: 70–73.
- Manchester, S. R. 1999. Biogeographical relationships of North American tertiary floras. *Ann. Mo. Bot. Gard.* 86: 472–522.
- McIver, S. B., and J. F. Sutcliffe. 1982. Sensilla of *Grylloblatta campodeiformis* Walker, pp. 137–157. *In* H. Ando [ed.], Biology of the Notoptera. Kashiyo-Insatsu, Nagano, Japan.
- Meyen, S. V. 1987. Fundamentals of palaeobotany. Chapman & Hall, London.
- Nagashima, T., H. Ando, and G. Fukushima. 1982. Life history of *Galloisiana nipponensis*, pp. 43–59. *In* H. Ando [ed.], Biology of the Notoptera. Kashiyo-Insatsu, Nagano, Japan.
- Nalepa, C. A., and C. Bandi. 1999. Phylogenetic status, distribution, and biogeography of *Cryptocercus* (Dictyoptera: Cryptocercidae). *Ann. Entomol. Soc. Am.* 92: 292–302.
- Nalepa, C. A., G. W. Byers, C. Bandi, C., and M. Sironi. 1997. Description of *Cryptocercus clevelandi* (Dictyoptera: Cryptocercidae) from the northwestern United States, molecular analysis of bacterial symbionts in its fat body, and notes on biology, distribution, and biogeography. *Ann. Entomol. Soc. Am.* 90: 416–424.
- Namkung, J. 1982. The taxonomy of the Grylloblattodea and their distribution in Korea, pp. 29–42. *In* H. Ando [ed.], Biology of the Notoptera. Kashiyo-Insatsu, Nagano, Japan.
- Plunkett, G. M., D. E. Soltis, and P. S. Soltis. 1997. Clarification of the relationship between Apiaceae and Araliaceae based on *matK* and *rbcl* sequence data. *Am. J. Bot.* 84: 567–580.
- Pritchard, G., and Scholefield, P. 1978. Observations on the food, feeding behaviour, and associated sense organs of *Grylloblatta campodeiformis* (Grylloblattodea). *Can. Entomol.* 110: 205–212.
- Qiu, Y.-L., J. Lee, F. Bernasconi-Quadroni, D. E. Soltis, P. S. Soltis, M. Zanis, E. A. Zimmer, Z. Chen, V. Savolainen, and M. W. Chase. 1999. The earliest angiosperms: evidence from mitochondrial, plastid and nuclear genomes. *Nature (Lond.)* 402: 404–407.
- Rasnitsyn, A. P. 1976. Grylloblattidae are the modern members of the order Protoblattodea (Insecta). *Dokl. Akad. Nauk. SSSR* 228: 273–275.

- Rasnitsyn, A. P. 1980. Order Grylloblattida. In B. B. Rohdendorf and A. P. Rasnitsyn [eds.], Historical development of class Insecta. Trans. Paleontol. Inst. 175: 150–154 [in Russian].
- Rasnitsyn, A. P., and V. A. Krassilov. 1996. Pollen in the gut contents of fossil insects as evidence of coevolution. Paleontol. J. 30: 716–722.
- Rentz, D.C.F. 1982. A review of the systematics, distribution and bionomics of the North American Grylloblattidae, pp. 1–18. In H. Ando [ed.], Biology of the Notoptera. Kashiyo-Insatsu, Nagano, Japan.
- Storozhenko, S. Y. 1988. A review of the family Grylloblattidae (Insecta). Articulata 3: 167–182.
- Storozhenko, S. Y. 1989. New and little-known Mesozoic grylloblattids (Insecta). Paleontol. J. 22(4): 45–52.
- Storozhenko, S. Y. 1991. New Permian and Mesozoic insects (Insecta, Grylloblattida: Blattogryllidae, Geinitziidae) from Asia. Paleontol. J. 24(4): 53–61.
- Storozhenko, S. Y. 1992. Permian fossil insects of north-east Europe: new and little-known Ideliidae (Insecta, Plecopteroidea, Grylloblattida). Entomol. Fenn. 3: 21–39.
- Storozhenko, S. Y. 1994. New Triassic grylloblattids from Kirghizia. Spixiana 17: 27–35.
- Storozhenko, S. Y. 1996a. New Upper Carboniferous grylloblattids (Insecta, Grylloblattida) from Siberia. Far East. Entomol. 26: 18–20.
- Storozhenko, S. Y. 1996b. New Triassic grylloblattids of the family Ideliidae (Plecopteroidea, Grylloblattida). Russ. Entomol. J. 5: 13–19.
- Storozhenko, S. Y. 1997. Classification of the order Grylloblattida (Insecta), with description of new taxa. Far East. Entomol. 42: 1–20.
- Storozhenko, S. Y. 1998. Systematics, Phylogeny and Evolution of the Grylloblattida (Insecta: Grylloblattida). Dal'nauka, Vladivostok [in Russian].
- Szeptycki, A. 1997. *Galloisiana sofiae* sp. n., a new species of Grylloblattodea from northern Korea. Pol. Pismo Entomol. 57: 257–262.
- Taylor, T. N., and E. A. Taylor. 1993. The biology and evolution of fossil plants. Prentice-Hall, Englewood Cliffs, NJ.
- Traverse, A. 1988. Paleopalynology. Unwin Hyman, Boston.
- Walker, E. M. 1937. *Grylloblatta*, a living fossil. Trans. R. Soc. Canada 26: 1–10.
- Zavada, M. S. 1991. The ultrastructure of pollen found in the dispersed sporangia of *Arberrella* (Glossopteridaceae). Bot. Gaz. 152: 248–255.

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