

Mimicry in the Triassic Madygen forest

Мимикрия в триасовом лесу Мадыгена

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KEY WORDS: Triassic, paleoecology, Blattoidea, insect-plant interactions, ferns, pteridosperms, mimicry.

КЛЮЧЕВЫЕ СЛОВА: триас, палеоэкология, блаттоидеи, взаимодействие насекомых и растений, папоротники, птеридоспермы, мимикрия.

*Postscript and dedication to the 100th Anniversary of A.G. Sharov,
an outstanding Russian paleontologist*

ABSTRACT. The paper deals with the putative example of mimicry between the blattoid insect *Sogdoblatta* and some plants with the pinnate foliages, first of all osmundacean ferns of the *Cladophlebis* genus. This example is based on the material collected from the famous Middle to Upper Triassic Madygen locality, disposed in Kirgizstan. The mimicry was formed by same shape of the blattoid forewings and the pinnules (ultimate segments, or segments of last order) of the pinnate plant leaves, same pattern of venation and same size of the forewings and leaf pinnules. Most probably this camouflage adaptation was aimed for hiding tactics of *Sogdoblatta* for avoiding being attacked by the insect-eating reptiles of Madygen, such as *Sharovipteryx* or *Longisquama*.

How to cite this paper: Naugolnykh S.V. 2024. Mimicry in the Triassic Madygen forest // Arthropoda Selecta. Vol.33. No.1. P.97–105. doi: 10.15298/arthscl.33.1.09

РЕЗЮМЕ. Статья посвящена возможному примеру мимикрии таракана *Sogdoblatta* и некоторых растений с перистыми листьями, прежде всего, осмундовых папоротников рода *Cladophlebis*. Этот пример основан на материале, собранном из знаменитого местонахождения Мадыген, расположенного в Киргизии. Мимикрия была сформирована/обусловлена одинаковой формой надкрыльев таракана и перышек (сегментов последнего порядка) перистых листьев растений, идентичными элементами жилкования, одинаковым размером надкрыльев и перышек листьев. Скорее всего, эта маскировочная адаптация была направлена на обеспечение тактики скрытности *Sogdoblatta* для избежания возможности быть атакованной насекомоядными рептилиями, такими как *Sharovipteryx* или *Longisquama*.

Introduction

In 2021th we celebrated 100th birth anniversary of the outstanding Russian paleontologist Alexander Grigorievich Sharov.

A.G. Sharov is a very well-known scientist, which name sounds very familiar to broad scientific public due to his brilliant contributions to classic paleoentomology, paleoecology [Sharov, 1973], and paleoherpetology [Sharov, 1970, 1971a, b]. Paleoecological studies related to the insect/plant interactions were always in the center of scientific activity of A.G. Sharov [1972].

A.G. Sharov had left a bright trace in paleontology as a great field worker, who together with a team of colleagues excavated such famous localities of fossil organisms as the Lower Permian (Kungurian) strata of the Chekarda locality, disposed in the Perm region, the Urals, Jurassic lymnic deposits of the Karatau Range, Kazakhstan, and the Triassic locality of Madygen, Kirgizstan, which is world-famous site because of numerous fossil plants, insects and reptiles found there [Sharov, 1970, 1971a, b]. Publications of A.G. Sharov are always marked as being written by scientifically correct language, precise estimations, nice set of photo-images of high quality, and artistically attractive line-drawings including reconstructions of the studied paleontological objects.

As it was noted above, the localities studied by A.G. Sharov contain not only insects, but very abundant plant micro- and macrofossils also.

Terrestrial plants since the very moment of their appearance in the Earth history were closely incorporated into interaction with other components of the paleoecosystems, i.e. paleoclimate, soils, atmospheric precipitation, and of course with the arthropods, which were important symbionts of the land plants practically for all time of their history. This plant/arthropod interaction was “polyvalentic”, both positive (co-evolution) and negative (herbivory). The most important basic interactions between arthropods and plants were reflected in trophic links or diet of herbivorous arthropods [Wiens, 1978; Wedmann *et al.*, 2007], but some other links also were evolutionary significant and played a notable role in construction of paleoecosystems.

One of such links between arthropods (mostly insects) and higher plants was a mimicry, i.e. camouflage behavior

allowing a potential prey to hide, or in contrast to prepare a hidden trap by carnivorous insect. Such camouflage tactics allowed insects to have the considerable priorities in struggle for life. It is a very good example of high potentiality of the paleontological material not just for descriptive morphology but for reconstruction of behavior even [Seilacher, 1967]. The first unequivocal examples of mimicry came from the low latitude Carboniferous forests (see Discussion below), but later this coevolutionary tendency wide developed and was reported from antitropical zones as well [Cuneo, 1986].

As it was already briefly mentioned above, one of the most important and bright results in scientific biography of A.G Sharov, was his excavation of the Middle to Late Triassic Madygen locality [Sharov, 1970, 1971a, b]. The present paper is focused on new evidence on the Madygen paleoecology.

Material and methods

The specimens in hand were collected independently by D.N. Esin (Moscow Lomonosov State University) in 1987 and V.V. Masjutin (Vjatka Paleontological Museum, the City of Kirov) in 1995 from the Madygen section (the Jailiochyo Site), Kirgizstan.

The Madygen section is a famous paleontological site, which can be regarded as internationally important place of the paleontological heritage [Sharov, 1970, 1971a, b; Vishnyakova, 1998]. According to the present-day stratigraphic concept, the deposits outcropped in the Madygen section should be regarded as Middle Triassic to Upper Triassic (i.e. stratigraphically more or less synchronous to Keuper of the Western and Central Europe [Dobruskina, 1980: 54; 1982]). Exceptional preservation of the numerous fossils, as well as their high diversity, allows to consider the Madygen locality as a good example of geological monuments of international value [Bruno *et al.*, 2014].

The Madygen locality, as it will be cited below, is disposed in the southern part of the Fergana valley, between the rivers Kradarjya on north and Zeravshan on south [Dobruskina, 1980, fig. 23].

The source strata are represented by thin intercalations of platy siltstones and fine-grained sandstones of bright orange to pale-yellow color. The strata belong to the Madygen Formation [Dobruskina, 1980]. The dominant mode of preservation of fossils are imprints (Figs. 1, A; 3, A–C; 4, A), although natural molds (Fig. 1, D) and compressions (Fig. 1, B) or imprints with the partly preserved compressed tissues (Fig. 1, B) are present at the locality as well.

The putative reconstruction of mimicry behavior of *Sogdoblatta* is prepared on the basis both detailed line-tracing drawing of *Cladophlebis* sp. leaves and line-tracing technique of de-covering of the wing venation of *Sogdoblatta* on the basis of the material in hand.

Observations

Paleofloristic assemblage of the Madygen section

Paleofloristic assemblage of the Madygen section has been discussed for a long time, but conventional taxonomical list of the plant taxa found in this section is not completely fulfilled yet. The most convincing list of the Madygen flora was published by I.A. Dobruskina [1982].

The assemblage is known mostly from the Jailiochyo site and includes both pteridophytes s.l., and various gymnosperms (Fig. 1, A–D).

The most common component of the Madygen flora was represented by numerous equisetophytes, mostly assigned to the genus *Neocalamites* Halle (Fig. 1, C). The *Neocalamites carrerei* (Zeiller) Halle (= *Phyllothea longifolia* Sixtel) stems of the Madygen locality are often leafy, with the numerous long linear leaves typical of many (but not all) representatives of this genus [Sixtel, 1966], although the naked stems with the nodal scars of lateral branches occur as well (Fig. 1, C). Ferns of the Madygen paleofloristic assemblage were attributed to the genus *Cladophlebis* Brongniart [Dobruskina, 1982, see here Fig. 2]. Now, the most representatives of *Cladophlebis* are regarded as belonging to the family Osmundaceae [Anderson, Anderson, 2008].

The Madygen flora includes rare representatives of arborescent lycopodiophytes of the genus *Ferganodendron* Dobruskina having long and complicated story of study and interpretation [Sixtel, 1962; discussion see in: Dobruskina, 1974, 1985; Naugolnykh, 2013]. The specimens in hand (see, for instance, Fig. 1, D) demonstrate all the characteristic features typical of this genus. Presence of the relatively large isoetopsid lycopodiophytes in the Madygen flora can be interpreted as the last phase of Triassic post-crises recovering of the vegetation [Fuchs *et al.*, 1991; Wang Zi-qiang, 1996; Gall *et al.*, 1998; Grauvogel-Stamm, 1999].

Gymnosperms of the Madygen locality are highly diverse, but many of them are still poorly studied. Pinnate leaves of *Vittaeophyllum* Dobruskina (Fig. 1, A) and *Lepidopteris* Schimper (Fig. 1, B) are the most common elements. Female reproductive organs of *Peltaspermum*-type probably belonging to the same parent plants are known from the same locality [Sixtel, 1962], and altogether (i.e., leaves, microstrobili, and “megasporephyllous” ovulate discs) were described as *Lepidopteris parvula* Sixtel [Sixtel, 1962: 316–319, figs 9–11].

Besides that, the Madygen flora contains many leaves of ginkgophyte affinity, i.e. simple lanceolate leaves of *Glossophyllum*-type), deeply-dissected cuneate leaves of *Sphenobaiera*, fan-shaped to palmate leaves of *Baiera*-type, but all of them are in need of serious and detailed revision.

Regarding the main scope of the present paper, the pinnate leaves of *Cladophlebis*, *Vittaeophyllum* and *Lepidopteris* are of special interest. They are discussed below in more details.

Blattoids from the Madygen section

The cockroaches of the Madygen section are discussed in the fundamental work by V.N. Vishnyakova [1998]. The taxonomical list of the cockroaches described by V.N. Vishnyakova includes following taxa: *Sogdoblatta nana* Vishnyakova, *S. maxima* Vishnyakova, *S. porrecta* Vishnyakova, *Thuringoblatta sogdianensis* Vishnyakova. The collection, which I have in my possession, includes thirty specimens of blattoid affinity. Five of them are fig-

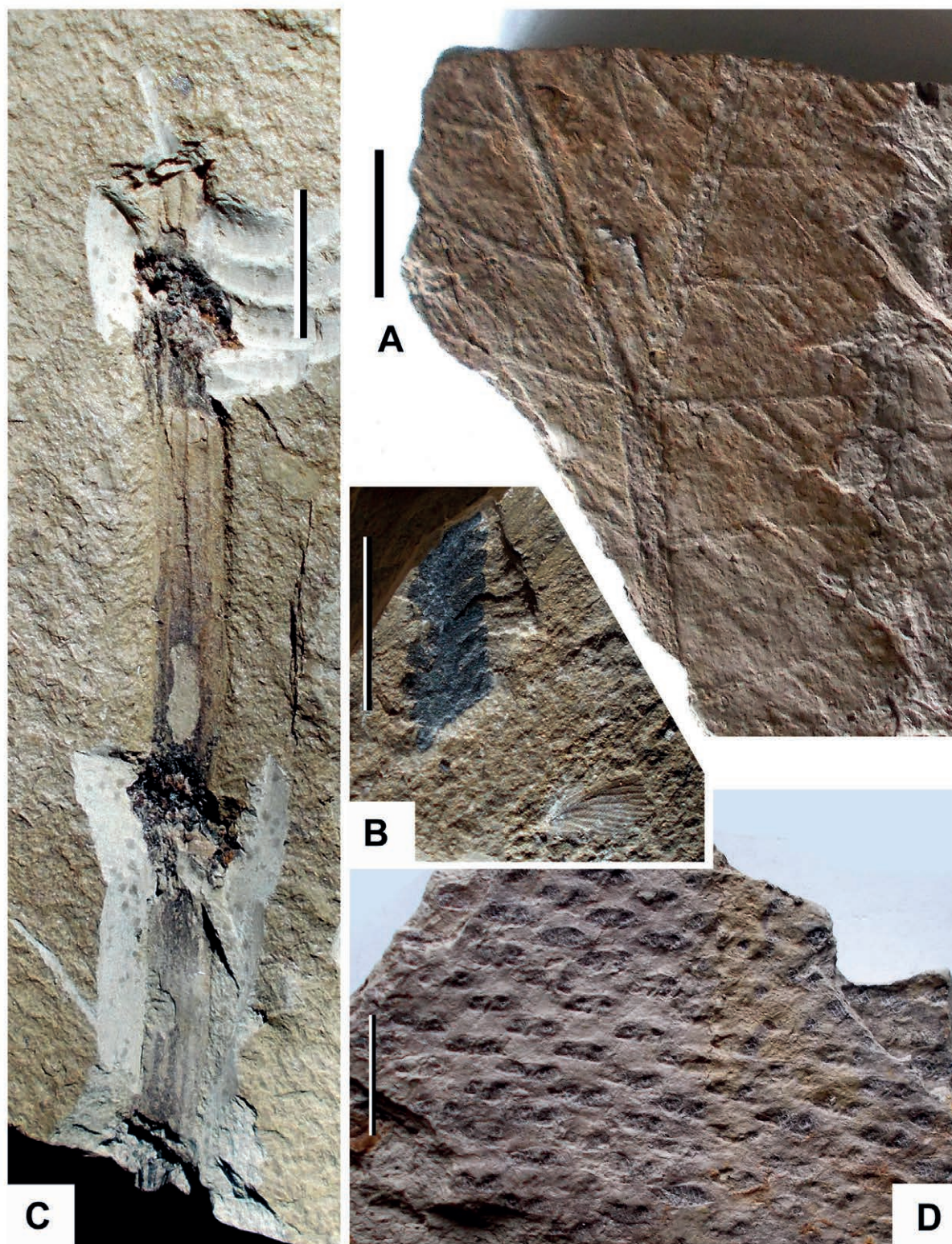


Fig. 1. Paleofloristic assemblage of the Madygen section. A, B — peltaspermean pteridosperms, A — *Vittaeophyllum hirsutum* (Sixtel) Dobruskina; B — pinna of *Lepidopteris* sp. and a wing of the insect *Incertae Sedis*; C — equisetophyte *Neocalamites* sp., D — isoetalean lycopodiophyte *Ferganodendron sauktangensis* (Sixtel) Dobruskina. Locality: Madygen. Scale bar is 1 cm.

Рис. 1. Палеофлористический комплекс разреза Мадыген. А, В — пельтаспермовые птеридоспермы, А — *Vittaeophyllum hirsutum* (Sixtel) Dobruskina; В — перо *Lepidopteris* sp. и крыло насекомого *Incertae Sedis*; С — хвощевидное *Neocalamites* sp., D — изозтовое плауновидное *Ferganodendron sauktangensis* (Sixtel) Dobruskina. Местонахождение: Мадыген. Масштаб 1 см.

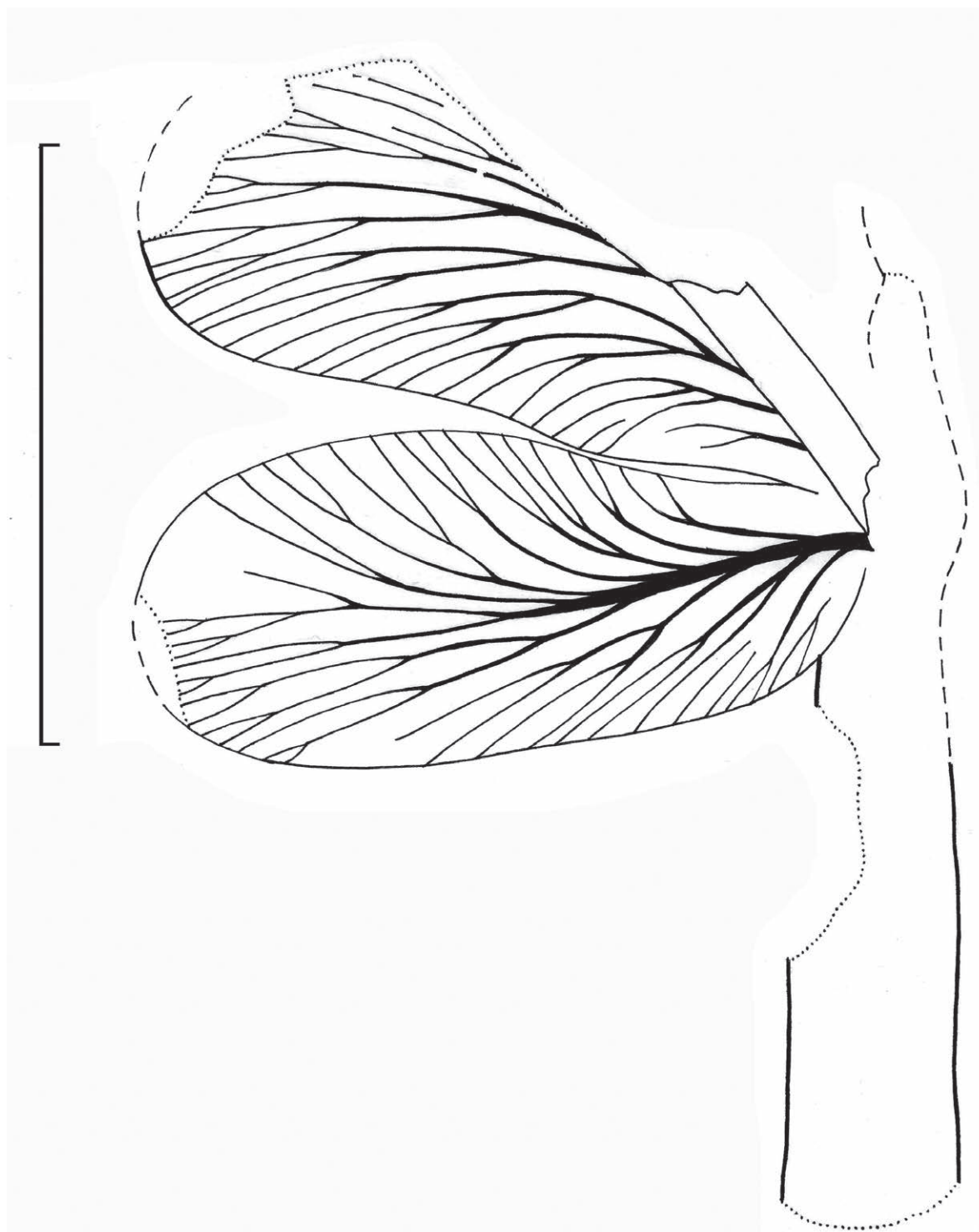


Fig. 2. *Cladophlebis* sp. a part of the fern frond; line tracing after: Dobruskina, 1982, Fig. 28, g; Plate XXIV, figs 5, 5a, 6). The Madygen section. Scale bar is 1 cm.

Рис. 2. *Cladophlebis* sp. часть вайи папоротника, прорисовка по: Dobruskina, 1982, Fig. 28, g; Plate XXIV, figs 5, 5a, 6). Масштаб 1 см.

ured in the present paper (Figs 3, 4). All the specimens are characterized by one and the same mode of preservation. They are preserved as fine imprints or natural molds. No organic tissues are present.

Careful comparison of the material in hand with the cockroaches from the Madygen section figured by V.N.

Vishnyakova [1998] allowed to determine three specimens in open nomenclature as *Sogdoblatta* sp. (Fig. 3, A–C) and two more or less complete specimens (Fig. 4, A, B) were assigned to *Sogdoblatta* cf. *porrecta* Vishnyakova. But we also should take in account the opinion by Peter Vrsasinsky (Earth Science Institute of the Slovak

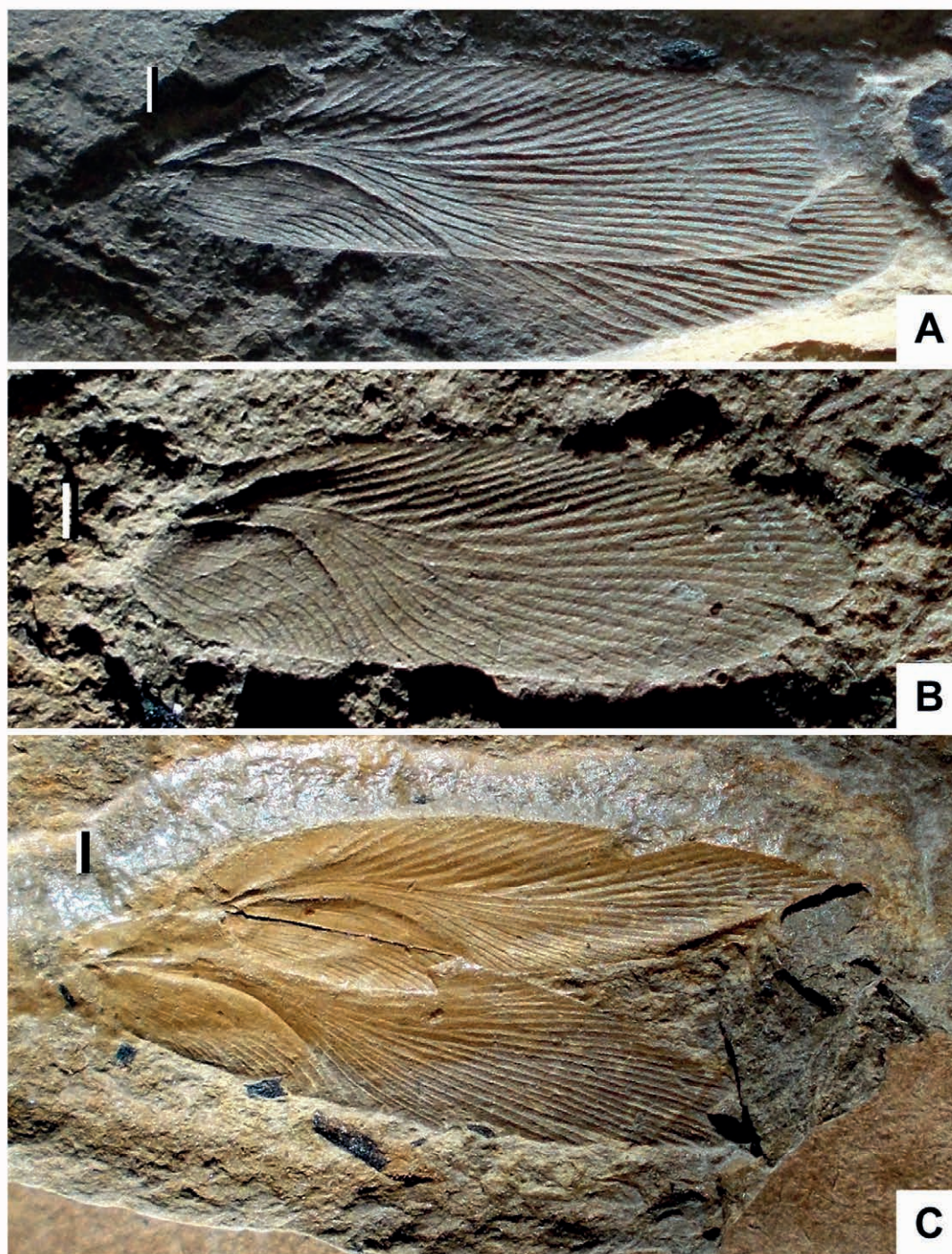


Fig. 3. Blattoid *Sogdoblatta* sp. The wing morphology. The Madygen section. Scale bar is 1 mm.

Рис. 3. Таракан *Sogdoblatta* sp. Строение крыльев. Местонахождение Мадыген. Масштаб 1 мм.

Academy of Sciences, Bratislava), who believes (personal communication) that the blattoid fauna of the Madygen section needs a serious revision.

All the blattoid taxa figured in the present paper show remarkable similarity with the separate segments of the last order (the pinnules) of the “pteridophyllous” pinnate leaves from the same locality, especially with the pinnules of *Cladophlebis* sp.

Mimicry

Careful comparison of the *Sogdoblatta*-wing venation with the venation of pteridophyllous leaves from the Madygen locality, especially with the *Cladophlebis*-type leaves, unequivocally shows that both of them have one and the same venation pattern.

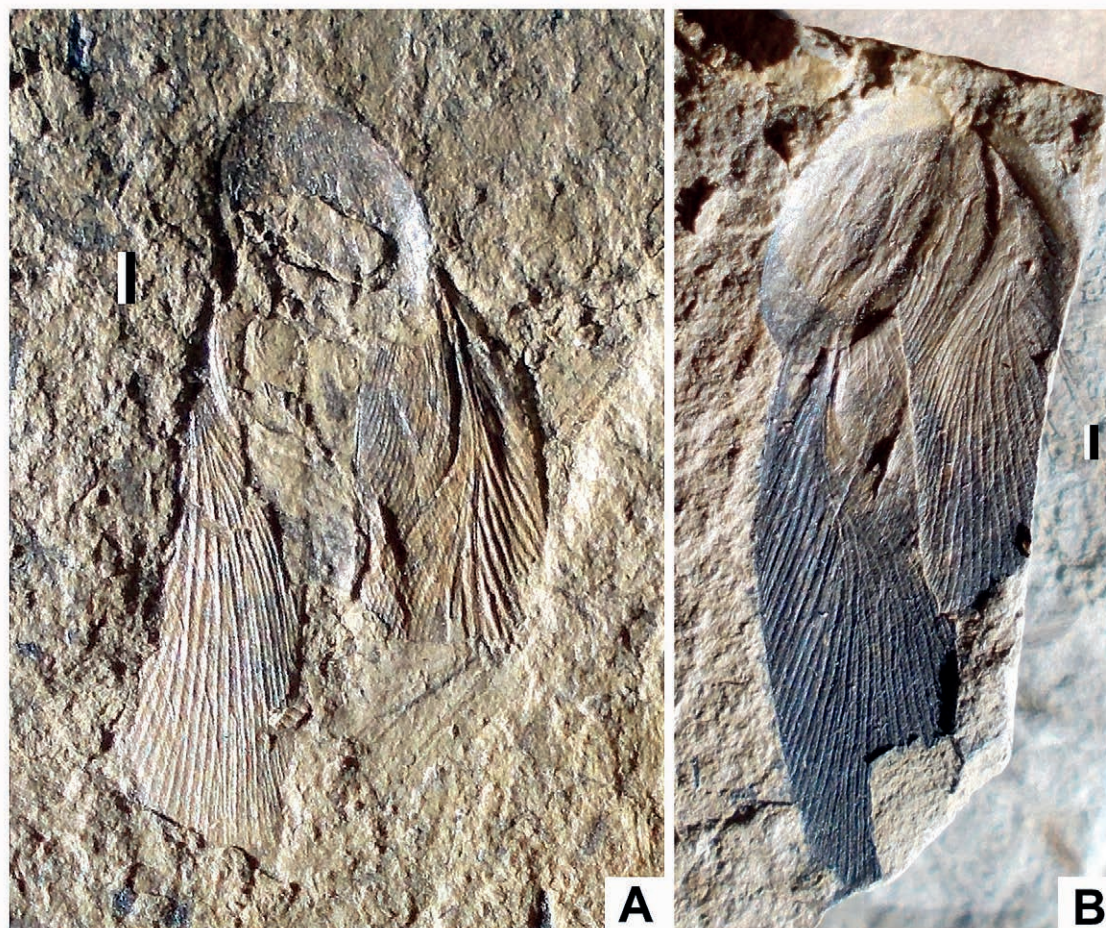


Fig. 4. Blattoid *Sogdoblatta* cf. *porrecta* Vishnyakova, 1998. The Madygen section. Scale bar is 1 mm.

Рис. 4. Таракан *Sogdoblatta* cf. *porrecta* Vishnyakova, 1998. Местонахождение Мадыген. Масштаб 1 мм.

First of all, we should note the slightly asymmetrical conditional “middle vein” or axial cluster of veins, which disposed somewhat anteriorly both in the *Cladophlebis* pinnules (Fig. 2), and the *Sogdoblatta* forewings (Figs 3, 4). The angles of dichotomy or divaricating of secondary/lateral veins of both are exactly the same. Anterior/acrosopic veins both of *Cladophlebis* pinnules and comparable veins of the *Sogdoblatta* forewings derived in wider angle approximately about 35–40°. These veins are disposed relatively randomly for both taxa. The posterior veins (basiscopic or caradromous veins of *Cladophlebis*) derive under narrower angle about 25–30°, and are disposed notably denser. Apical margins of the *Sogdoblatta* forewings are round and repeat shape and size of the apical part of the *Cladophlebis* pinnules. One more important feature, which is the same both for the *Cladophlebis* pinnules and *Sogdoblatta* forewings is a general pattern of the veins branching. Most of the veins of both taxa are once to twice dichotomizing, although simple veins occur for both taxa as well. Finally, general shape, proportions, and size both of the *Cladophlebis* pinnules and *Sogdoblatta* forewings are practically the same.

It should be noted that there are some other plants with the pinnate leaves in the Madygen flora, pinnules of which

morphologically can be comparable with the *Cladophlebis* pinnules and have considerable resemblance with the *Sogdoblatta* forewings. Such plants include, for instance, *Kugartenia irregularis* Sixtel [Sixtel, 1960, Plate 9, fig. 1, text-fig. 9], “*Odontopteris*” (?) *latiloba* Sixtel [Sixtel, 1962, Plate XIX, fig. 14, text-fig. 23], *Tersiella radczenkoi* Sitel [Sixtel, 1962, Plate XIX, figs 7–13, Plate XX, figs 1–5, text-fig. 25, please, pay a special attention to the shortened apical pinnules], *Thinnfeldia minima* Sixtel [Sixtel, 1962, Plate XX, figs 6–8], *Madygenia asiatica* Sixtel [Sixtel, 1962, Plate XXII, figs 7, 8], “*Neuropteridium*” (?) *ferganicum* Sixtel [Sixtel, 1962, Plate XIX, figs 3–5, text-fig. 31], *Ctenopteris punctata* Sixtel [Sixtel, 1962, Plate XDIX, figs 5–6, text-fig. 32].

It is no question that the blattoids were well-adopted for hiding inside the plant debris on the forest ground, which was both a rich source for food and a shelter for effective hiding (Günter, 1989), but this fact doesn’t contradict a hypothesis that at least some of the blattoids were evolved in a context of mimicry and/or similar adaptations in more or less dense forest canopy.

Thus, all the morphological similarities listed above, according to the present author’s viewpoint can be interpreted as a result of mimicry aimed for hiding of the

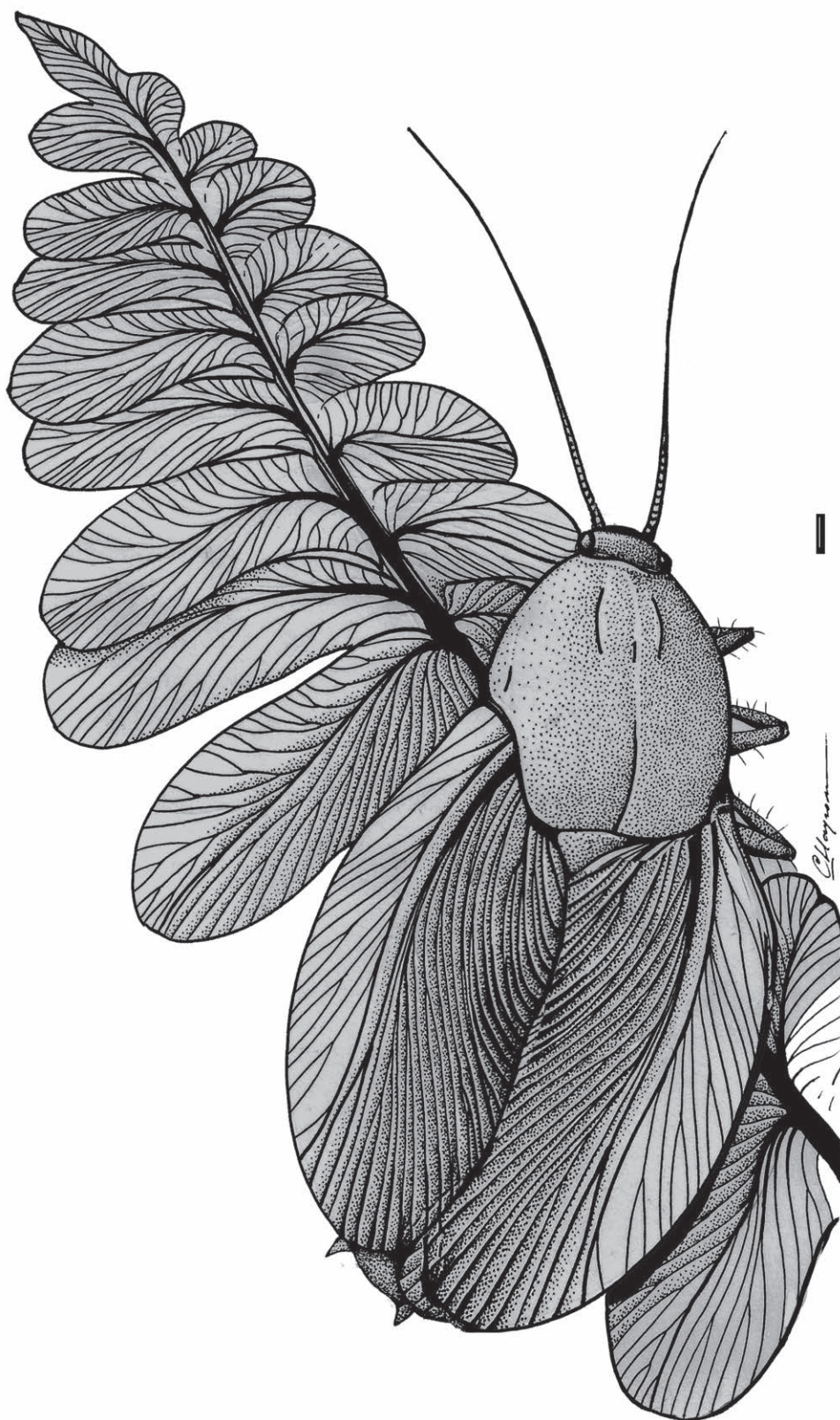


Fig. 5. Blattoid *Sogdoblatta* cf. *porrecta* Vishnyakova, 1998 using mimicry behavior on the fern frond *Cladophlebis* sp. Scale bar is 1 mm.

Рис. 5. Таракан *Sogdoblatta* cf. *porrecta* Vishnyakova, 1998 использующий мимикрию на листе папоротника *Cladophlebis* sp. Масштаб 1 мм.

Sogdoblatta insect inside the foliage of *Cladophlebis* and other similar plants with the pinnate fronds (peltaspermalean pteridosperms for instance) for making the insect practically undifferentiated inside the forest underbrush canopy. Such adaptation can be highly effective in the Middle to Late Triassic Madygen forest inhabited by many insect-eating reptiles, such as *Sharovipteryx mirabilis* (Sharov) and *Longisquama insignis* Sharov.

Discussion

There is a number of examples of mimicry, which were reported on the basis of the fossil material. First of all we should cite a classic example of mimicry of the *Phyllomilacris* cockroach from the Upper Carboniferous deposits bearing forewings repeating venation of the trigonocarpalean (Medullosales) pteridosperm *Neuropteris* [Scott, Taylor, 1983]. In a broad aspect the *Phyllomilacris/Neuropteris* mimicry is very similar to the *Sogdoblatta/Cladophlebis* case. Taking in account the fact that some similar “pair” examples of mimicry are known for the Permian time as well (*Kunguroblattina/Permo-callipteris*; see for details: Naugolnykh [2017]), we can conclude that the “mimicrid pair” blattoid/pteridosperm and/or blattoid/fern appeared at least in Carboniferous and existed further during Permian and Triassic periods till the pteridosperms became decrease in their number and diversity in the middle of Mesozoic.

Among the insects of Permian period there is one more example of mimicry between the scorpion fly (Mecoptera, Permochoristidae) *Petromantis sylvanensis* Martynov and spenophylls *Sphenophyllum biarmicum* Zalessky emend. Naug. and closely related *S. comiense* Tchirkova [Naugolnykh, 2003, 2015, 2017]. In Mesozoic, intensification of co-evolution processes between plants and insects resulted in appearance of new numerous examples of mimicry, such as an early representative of Lepidoptera *Undopterix sukatchevae* Skalski and preanthophyte/preangiosperm bracts [Krassilov, 2003].

To sum up, we can underline that the mimicry of *Sogdoblatta/Cladophlebis* fits well to the general tendency of co-evolution of plants and insects in Late Paleozoic – Early Mesozoic phase of development of the sophisticated terrestrial ecosystems.

Acknowledgements. The author is thankful to Peter Vrsansky (Earth Science Institute of the Slovak Academy of Sciences, Bratislava, Slovakia) for his valuable discussion of the taxonomical attribution of the blattinopsid remains of the collection studied. Special thanks are due to providing of the material for present study by colleagues D.N. Esin (Moscow Lomonosov State University) and V.V. Masjutin (Kirov Paleontological Museum, Kirov, Russia). The work is fulfilled in a framework of the State Program of the Geological Institute of Russian Academy of Sciences. The author is grateful to K.G. Mikhailov (Zoological Museum of Moscow Lomonosov State University, Moscow) and one anonymous reviewer (Zoological Institute of RAS, Saint-Petersburg) for the constructive and valuable advice and comments.

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Responsible editor K.G. Mikhailov