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# New and Little-Known Grylloblattids of the Family Geinitziidae (Insecta: Grylloblattida) from the Triassic and Jurassic of Europe, Asia, and South Africa

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**Abstract**—The fossil history of the family Geinitziidae is reviewed. New taxa are described in the family: *Shurabia hissarica*, sp. nov. (Lower Jurassic of Tajikistan), *Sh. shartegica*, sp. nov. (Upper Jurassic of Mongolia), *Sh. serrata*, sp. nov. and *Ginitzia sagulensis*, sp. nov. (both Lower Jurassic of Kyrgyzstan). The subfamily Stegopterinae Sharov, 1961 is synonymized under Geinitziinae Handlirsch, 1906. The genera *Minesedes* Fujiyama, 1973 and *Ominea* Fujiyama, 1973 (Upper Triassic of Japan) are synonymized under *Shurabia* Martynov, 1937 and *Geinitzia* Handlirsch, 1906, respectively. *Geinitzia varia* Bode, 1953 (Lower Jurassic of Germany) and *Fletchizia picturata* Riek, 1976 (Upper Triassic of South Africa) are redescribed from their holotypes. *F. kapokraalensis* Wappler, 2001 and *F. aleda* Wappler, 2001 (both Upper Triassic of South Africa) are transferred to the genus *Shurabia*.

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*Key words*: new species, Geinitziidae, Insecta, Grylloblattida, Triassic, Jurassic, Europe, Asia, South Africa.

## INTRODUCTION

The earliest grylloblattids are known from rare low-diversity Upper Carboniferous fossils (Storozhenko, 1997, 1998, 2002). The abundance and diversity of grylloblattids abruptly increases in the Early Permian, when the order Grylloblattida becomes the predominant taxon of insects to occupy this position until the end of the Middle Permian. During the Upper Permian, the diversity of grylloblattids distinctly decreases, reaching its local minimum in the Lower Triassic. However, the taxon is not actually fading away, since some of the Permian families reappear in the Middle and/or Upper Triassic. Another, stronger extinction starts in the Jurassic; extremely rare latest fossils of winged grylloblattids are described from the Lower Cretaceous (Aristov, 2005). Modern grylloblattids are rare wingless cryptobionts with low diversity, restricted in their distribution to the northern hemisphere. Twenty-six extant species are known, grouped into five genera within a single Grylloblattidae family (Jarvis and Whiting, 2006).

This work reviews the small family Geinitziidae Handlirsch, 1906, known from the Lower Permian to the Upper Jurassic. The review is based on previously published data (Fujiyama, 1973; Riek, 1976; Rasnitsyn, 1982; Storozhenko, 1998; Ansorge and Rasnitsyn, 2000; Wappler, 2001; Aristov, 2004, 2005) and on unpublished data of the authors.

The earliest rare Geinitziidae are known from the Middle Permian of the Kuznetsk and Pechora coal basins (Kuznetsk Formation and Rudnik Subformation of the Lek-Vorkuta Formation, respectively). The genus *Stegopteron* Sharov, 1961 found there was originally described as representing a monotypic family. The status of this taxon was subsequently lowered to subfamily Stegopterinae Sharov, 1961 within the family Geinitziidae (Aristov, 2004). New Geinitziidae material, especially *Shurabia hissarica* sp. nov. from the Lower Jurassic of Tajikistan, displays the principal diagnostic character of Stegopterinae: branches of RS in the forewing directed posteriorly, as in doubtless Stegopterinae, making the recognition of *Stegopteron* even as a separate subfamily superfluous. For this reason, we consider Stegopterinae Sharov, 1961 as a synonym of Geinitziinae Handlirsch, 1906 (syn. nov.).

The only Late Permian geinitziid is known from an unidentifiable incomplete impression (anterior portion of a wing) from the Novo-Aleksandrovka fossil site (Northern Dvina Stage, Orenburg oblast).

Early Triassic geinitziids are extremely rare, like the other Grylloblattida and insects in general. Several specimens of *Shurabia* were found in the Maltsevo For-

mation of Kemero oblast, which is considered as either Lower Triassic or Upper Permian.

In the Middle Triassic, species of the genus *Shurabia* are relatively abundant in the Madygen Formation (Ladinian or Carnian of Kyrgyzstan). In the Carnian coal mine Hazegatani (Momonoki Formation) near Omine in Japan, *Minesedes elegans* Fujiyama, 1973 and *Ominea reticulata* Fujiyama, 1973 were found. These impressions display some unusual features of R and RS in comparison with other geinitziids. Nevertheless, *Shurabia* sometimes displays also irregular branching of R and anterior crest of RS branches, allowing to synonymize *Minesedes* under *Shurabia* (syn. nov.). *Ominea* Fujiyama, 1973 displays the diagnostic character of *Geinitzia* Handlirsch, 1906, namely, the three-branched $CuA_1$, and is therefore synonymized here under *Geinitzia* (syn. nov.).

Middle Triassic *Nivopteria nanshenguensis* Lin, 1978 and *Tomia fuyanensis* Lin, 1978 from the Nanshenghu deposits in the Guizhou Province of China were described as members of the family Tomiidae (= Chaulioditidae) (Lin, 1978) and later transferred to the genus *Shurabia* (Storozhenko, 1998). However, a revision of Tomiidae showed that both taxa actually belong to this family (Aristov, 2003).

Late Triassic *Shurabia* are known from the lower Ipswich Formation (Queensland, Australia). *Shurabia* and endemic *Fletchizia* are described from the Molteno Formation (Karoo Basin, South Africa). Geinitziids were found at several sites here: Kapokraal, Tina Bridge (Eastern Cape Province) and Nieuwjaars Spruit (Orange Free State) (Riek, 1976; Wappler, 2001).

In the Lower Jurassic, the diversity of Geinitziidae increases and the relatively diverse *Geinitzia*, known from the sites Dumbleton (Gloucestershire, England) and Grassel and Hondelage (Braunschweig, Germany), appear. *G. supercauda* Bode, 1953 from Hondelage and *G. debilis* Handlirsch, 1906 from Mecklenburg (both from the Upper Toarcian of Germany) may rather belong to *Shurabia*; a reexamination of the holotypes is necessary to solve this problem.

In addition to *Geinitzia*, in the upper Lower Jurassic of Dobbertin in Germany, *Prosepididontus calopteryx* Handlirsch, 1920 was found (Handlirsch, 1920–1921; Ansorge and Rasnitsyn, 2000), originally described as representing a monotypic family within the order Trichoptera and later transferred to Geinitziidae. The structure of remigium in *Prosepididontus* is different from that in *Shurabia*, especially in the specimen of *Sh. angustata* Martynov, 1937 from the Cheremkhovo Formation of Irkutsk oblast (Russia) (Storozhenko, 1998, text-fig. 283), only in the posterior crest of RS branches. Anal area with anal veins confluent with each other and with CuP is unique among Geinitziidae and Grylloblattida in general, confirming the genus status of *Prosepididontus*.

Diverse Early Jurassic *Shurabia* were found at the sites Shurab II (Sulyukta Formation of Tajikistan), Sogyuty (Dzhil Formation of Kyrgyzstan), and Meixi (Menkoushan Formation, Jiangxi Province, China). In the Lower and Middle Jurassic deposits of the Sagul Formation of Sagul in Kyrgyzstan, *Shurabia* and *Geinitzia* were found. In the Cheremkhovo Formation of Ust'-Baley in Irkutsk oblast and in the Khamar-Khoburin Formation of the site Tushilga in Mongolia, only *Shurabia* are known. Middle Jurassic *Shurabia* are known from the site Kugitang (Kugitang Formation of Tajikistan). The latest Geinitziidae are known from the Upper Jurassic deposits of the site Shar-Teg (Shar-Teg Formation) in Mongolia. *Shurabia* is recorded in the Jurassic site Beienrode near Flechtorf in Germany.

Thus, the family Geinitziidae had a broad distribution both stratigraphically (from the Lower Permian to the end of Jurassic; the genus *Shurabia* being present during the entire Triassic and Jurassic) and geographically (its range including Central Europe, Siberia, Mongolia, China, Japan, Central Asia, South Africa, and Australia). The taxonomic diversity of the family is not very high: there are 34 species described in five genera (*Stegopteron*, *Shurabia, Geinitzia, Prosepididontus*, and *Fletchizia*). Geinitziids are rare in the Permian and not abundant in the Lower and the definite Middle Triassic; they are, however, common from the Late Triassic to the end of Jurassic.

## MATERIAL

The material examined, including the types, is stored in the Paleontological Institute of the University of Göttingen (PIUC), the Bernard Price Institute for Palaeontological Research (University of the Witwatersrand, Johannesburg; BP), the South African National Biodiversity Institute (Pretoria; PRE/F–SANBI), and the Borissiak Paleontological Institute of the Russian Academy of Sciences (PIN).

## SYSTEMATIC PALEONTOLOGY

Order Grylloblattida

Suborder Grylloblattina

**Family Geinitziidae Handlirsch, 1906**

**Genus *Geinitzia* Handlirsch, 1906**

***Geinitzia varia*: Bode, 1953**

*Geinitzia varia*: Bode, 1953, p. 33, pl. I, fig. 1; Storozhenko, 1997, p. 14; Storozhenko, 1998, p. 128, text-fig. 267.

*Hannoptera promota*: Bode, 1953, p. 38, pl. I, fig. 7 (synonymized by Storozhenko, 1997, p. 14).

Holotype. PIUC, no. 402-1, direct and counter impressions of incomplete forewing; Germany, env. Braunschweig, Hondelage site; Lower Jurassic, Lower Toarcian, Posidonia Shale.

Description (Figs. 1a, 2a). Medium-sized insects. Anterior margin of forewing weakly convex, costal field twice as broad as subcostal field. SC with ten simple and branching anterior branches, dichotomizing at the level of the distal end of SC. Median branching immediately behind the base of RS, MA

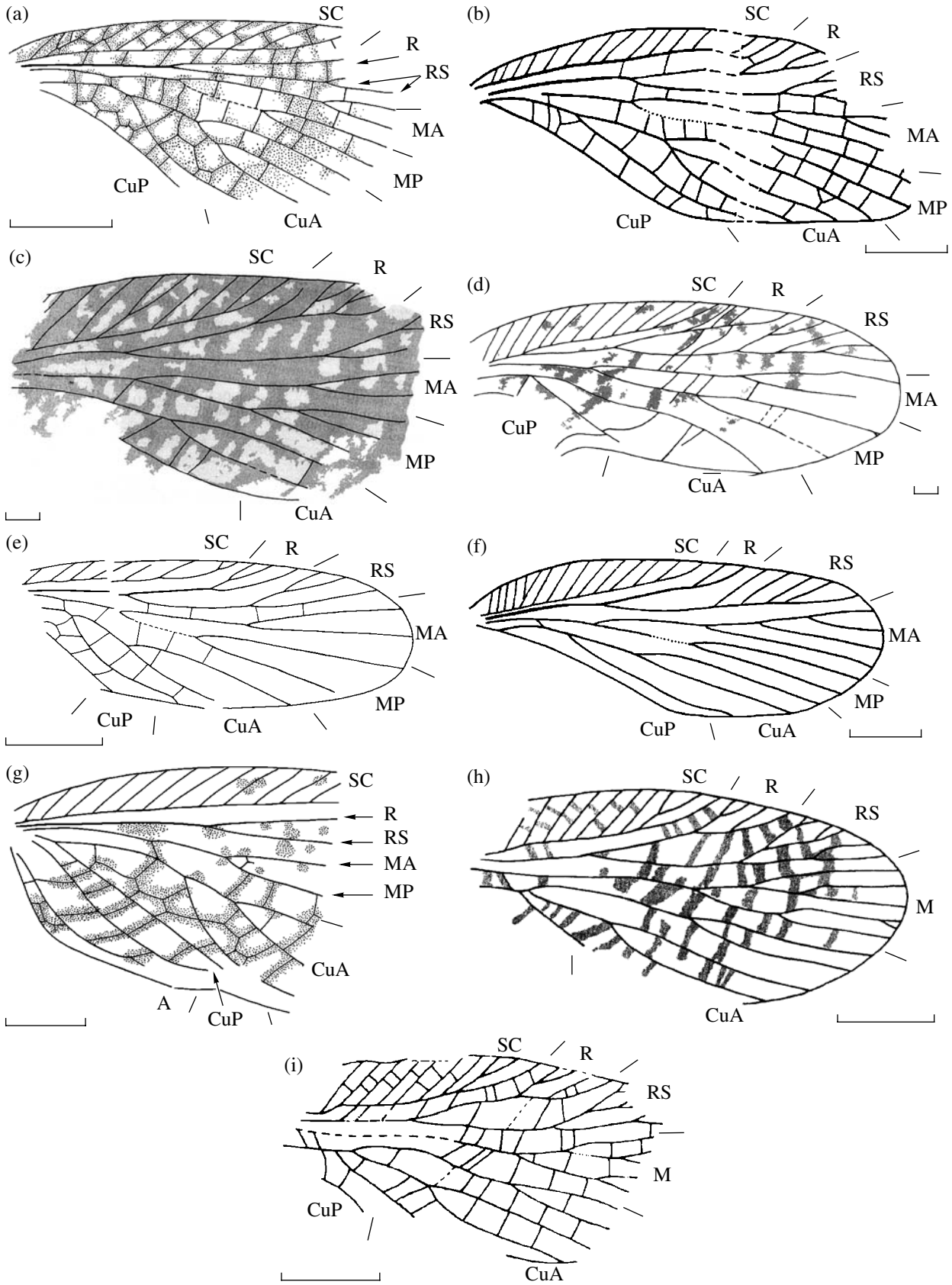
(a)
SC
R
RS
MA
MP
CuP
CuA
(b)
SC
R
RS
MA
MP
CuP
CuA
(c)
SC
R
RS
MA
MP
CuA
(d)
SC
R
RS
MA
CuP
MP
CuA
(e)
SC
R
RS
MA
MP
CuP
CuA
(f)
SC
R
RS
MA
MP
CuP
CuA
(g)
SC
R
RS
MA
MP
CuA
A
CuP
(h)
SC
R
RS
M
CuA
(i)
SC
R
RS
M
CuP
CuA

**Fig. 1.** Species of the family Geinitziidae: (a) *Geinitzia varia* Bode, 1953, holotype PIUC, no. 402-1, fossil site Hondelage; (b) *Geinitzia sagulensis*, sp. nov., holotype PIN, no. 3073/232, fossil site Sagul; (c) *Shurabia aleda* (Wappler, 2001), holotype PRE/F 19623a, fossil site Nieuwjaars Spruit; (d) *Shurabia kapokraalensis* (Wappler, 2001), holotype PRE/F 16418, fossil site Kapokraal; (e) *Shurabia hissrica*, sp. nov., holotype PIN, no. 3194/20, fossil site Kugitang; (f) *Shurabia serrata* sp. nov., holotype PIN, no. 2785/2161, fossil site Sagul; (g) *Shurabia shartegica*, sp. nov., holotype PIN, no. 4270/1939, fossil site Shar-Teg; (h, i) *Fletchizia picturata* Riek, 1976, holotype BP/2/20997, direct and counter impressions, fossil site Tina Bridge. Scale: (1a, 1e) 2 mm; (1b, 1f) 3 mm; (1c, 1d) 1 mm; (1h, 1i) 4 mm.

dividing into two branches at the level of the first bifurcation of RS; MP with two branches, bifurcating somewhat more proximal than MA. $M_5$ flowing into CuA prior to its branching; three branches of $CuA_1$ straight, CuA and CuP weakly curved. Transverse veins simple, forming two rows of cells in the intercubital field and in the field between the branches of CuA. Coloration patterned along transverse veins.

Measurements, mm. Length of forewing around 16.

Remarks. Bode (1953, p. 38) described also the hindwing of *Hannoptera promota*, later synonymized

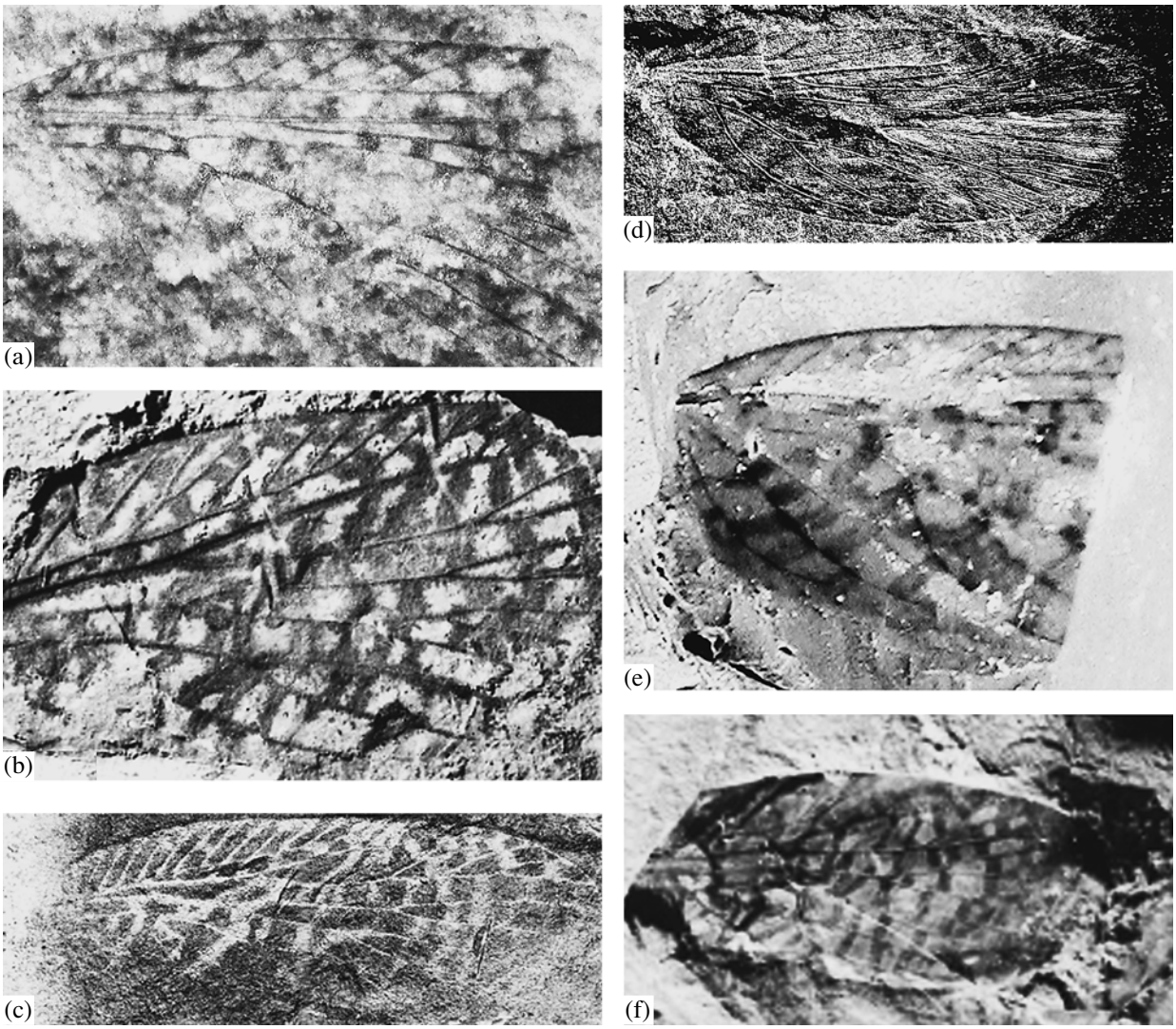


**Fig. 2.** Species of the family Geinitziidae: (a) *Geinitzia varia* Bode, 1953, holotype PIUC, no. 402-1, fossil site Hondelage, ×4; (b) *Shurabia aleda* (Wappler, 2001), holotype PRE/F 19623a, fossil site Nieuwjaars Spruit, ×8; (c) *Shurabia kapokraalensis* (Wappler, 2001), holotype PRE/F 16418, fossil site Kapokraal, ×4; (d) *Shurabia hissarica*, sp. nov., holotype PIN, no. 3194/20, fossil site Kugitang, ×7; (e) *Shurabia shartegica*, sp. nov., holotype PIN, no. 4270/1939, fossil site Shar-Teg, ×7; (f) *Fletchizia picturata* Riek, 1976, holotype BP/2/20997a, fossil site Tina Bridge, ×4.

under *G. varia* by Storozhenko (1998). However, several impressions of geinitziids were found at Hondelage site, and none of them included both fore- and hindwings. Thus, it is probably premature to consider the isolated hindwing from Braunschweig as belonging to the species described from the forewing.

Material. Holotype.

***Geinitzia sagulensis*** **Aristov, Wappler et Rasnitsyn, sp. nov.**

Etymology. From the name of the fossil site, Sagul.

Holotype. PIN, no. 3073/232, direct impression of deformed forewing without anal area; Kyrgyzstan, Batkenskii District, 15 km SE Shurab, Sagul site; Lower Jurassic, Sagul Formation.

Description (Fig. 1b). Medium-sized insects. Anterior margin of forewing convex, costal field twice as broad as subcostal field. SC with 15 or 16 dense simple anterior branches, ending in the distal third of the wing. R forming anterior crest of three branches. RS beginning proximal of the middle of the wing, dichotomizing, with four or more branches. Median bifurcating at the level of the base of RS, MA with three branches, not anastomosing with RS, MP with two branches. $CuA_1$ dividing into three branches proximal of its middle. $CuA_2$ and CuP weakly curved. Transverse veins simple and Y-shaped.

Measurements, mm. Length of forewing around 20.

Diagnosis. The new species is especially similar to *G. asiatica* Storozhenko, 1990 from the same fossil site (Storozhenko, 1990), from which it is distinguished by the free MA and the median bifurcating at the level of the base of RS.

Remarks. This specimen was identified earlier (Rasnitsyn, 1982) as *Shurabia angustata*, Martynov, 1937.

Material. Holotype.

## Genus *Shurabia* Martynov, 1937

***Shurabia aleda*: (Wappler, 2001), comb. nov.**

*Fletchizia aleda*: Wappler, 2001, p. 98, text-fig. 7

Holotype. PRE/F 19623a, b; direct and counter impressions of incomplete forewing; South Africa, Orange Free State, Nieuwjaars Spruit site; Karoo basin, Upper Triassic, Molteno Formation.

Description (Figs. 1c, 2b). Medium-sized insects. Anterior margin of forewing weakly convex; costal field almost four times as broad as subcostal field, crossed with ten simple and bifurcating branches of SC. R irregularly bifurcating, with six anterior branches. RS beginning in basal half of the wing, with three or more branches forming the posterior crest. Median dividing into branches at the level of the base of RS, MA with two branches, MP with three branches. $CuA_1$ with two branches, almost straight, $CuA_2$ curved. Transverse veins simple, coloration patterned along them.

Measurements, mm. Length of forewing around 20.

Remarks. This species is transferred into the genus *Shurabia* based on M bifurcating at the level of the base of RS and on the two-branched $CuA_1$.

Material. Holotype.

***Shurabia kapokraalensis*** **(Wappler, 2001), comb. nov.**

*Fletchizia kapokraalensis*: Wappler, 2001, p. 96, text-fig. 8.

Holotype. PRE/F 16418, direct impression of forewing; South Africa, Eastern Cape Province, Kapokraal site; Karoo basin, Upper Triassic, Molteno Formation.

Description (Figs. 1d, 2c). Medium-sized insects. Anterior margin of forewing convex; costal field almost four times as broad as subcostal field, crossed with 12 dense straight anterior branches of SC. R with four branches, forming the anterior crest. RS beginning in the basal half of the wing, with five long branches forming the anterior crest. Median divided into branches proximal of the base of RS, MA and MP with two branches. $CuA_1$ simple, weakly S-shaped, $CuA_2$ simple, distal half of the field between CuA branches strongly dilated. CuP curved. Transverse veins simple, coloration patterned along them.

Measurements, mm. Length of forewing around 21.

Remarks. This species is transferred into the genus *Shurabia* based on the absence of characters distinguishing the genus *Fletchizia* (more distal branching of M and polymerized CuA) and on the agreeing of the general venation pattern with that of the genus *Shurabia*.

Material. Holotype.

***Shurabia hissarica*** **Aristov, Wappler et Rasnitsyn, sp. nov.**

Etymology. From the name of the Hissar range.

Holotype. PIN, no. 3194/20, direct and counter impression of front wing without the anal area; Tajikistan, south-eastern branches of the Hissar, Maichalisay, Kugitang site; Lower Jurassic, Kugitang Formation.

Description (Figs. 1e, 2d). Small insects. Anterior margin of forewing weakly convex, costal field 1.5 times as broad as subcostal field. SC with eight sparse anterior branches, ending in distal third of the wing. R with three long anterior branches, forming the anterior crest. RS beginning proximal of wing middle, with three long anterior branches, forming the posterior crest. Median branching at the level of the base of RS; MA with two branches, bifurcating around its middle; MP with two branches, bifurcating somewhat proximal of MA. $M_5$ flowing into CuA proximal of its branching, $CuA_1$ bifurcating proximal of its middle, $CuA_2$

S-shaped. CuP straight, transverse veins simple and H-shaped in the intercubital field.

Measurements, mm. Length of forewing 9.

Diagnosis. The anterior crest of RS branches makes the new species especially similar to *Prosepididontus calopteryx* from the Lower Toarcian of Germany (Ansorge and Rasnitsyn, 2000) and to *Sh. ferganensis* from the Middle or Upper Triassic of Kyrgyzstan (Rasnitsyn, 1982), from which, as well as from all the other members of its genus, the new species differs in the shape of the anterior crest of R branches.

Remarks. Posterior crest of RS branches is typical to *Stegopteron* Sharov, 1961 and *Prosepididontus* Handlirsch, 1906, but the former genus lacks the S-shaped $CuA_2$, and the latter lacks anterior branches of R.

Material. Holotype.

#### *Shurabia serrata* Aristov, Wappler et Rasnitsyn, sp. nov.

Etymology. From the Latin *serrata* (saw-toothed).

Holotype. PIN, no. 2785/2161, direct impression of forewing without anal area; Kyrgyzstan, Batkenskii District, 15 km SE Shurab, Sagul site; Lower Jurassic, Sagul Formation.

Description (Fig. 1f). Medium-sized insects. Anterior margin of forewing strongly convex, costal field four times as broad as subcostal field. SC with 15 dense, simple, less often dichotomizing anterior branches, ending around wing middle. R bifurcating near apex. RS beginning under wing middle, forming regular posterior crest of five branches. Median dividing into branches at the level of the base of RS, MA forming regular crest of four branches, MP with two branches. $M_5$ flowing into CuA proximal of its bifurcation into branches; $CuA_1$ almost straight, dividing into branches anterior to the middle; $CuA_2$ S-shaped. CuP weakly curved.

Measurements, mm. Length of forewing 18.

Diagnosis. The new species differs from the other members of the genus in the combination of two-branched R and regular crests of RS and MA branches.

Material. Holotype.

#### *Shurabia shartegica* Aristov, Wappler et Rasnitsyn, sp. nov.

Etymology. From the name of Mount Shar-Teg.

Holotype. PIN, no. 4270/1939, direct impression of a fragment of forewing; Mongolia, Gobi-Altai Province east of Mount Atas-Bogd, 5–6 km west of Mount Shar-Teg; Upper Jurassic, Shar-Teg Formation.

Description (Figs. 1g, 2e). Medium-sized insects. Anterior margin of forewing convex, costal field three times as broad as subcostal field, crossed with straight anterior branches of SC. RS starting in basal half of the wing, median branching distal of the base of RS. $M_5$ flowing into CuA proximal of its branching, CuA dividing into $CuA_1$ and $CuA_2$ almost at the level of the base of RS. $CuA_1$ branching relatively close to base, $CuA_2$ smoothly curved, CuP straight. Apical portions of $A_1$ and $A_2$ curved towards wing apex. Transverse veins simple, forming two rows of cells in the intercubital field and in the field between CuA branches. Coloration including pattern along transverse veins and small spots.

Measurements, mm. Length of forewing around 13.

Diagnosis. The new species differs from all the other members of the genus in CuA branching relatively far from base and in the apical portions of $A_1$ and $A_2$ curved towards the apex of the wing.

Material. Holotype.

### Genus *Fletchizia* Riek, 1976

#### *Fletchizia picturata* Riek, 1976

*Fletchizia picturata*: Riek, 1976, p. 806, text-fig. 9, pl. 3, fig. 1; Storozhenko, 1998, p. 131, text-fig. 289.

Holotype. BP/2/20997a, b (C-M.F. I 256a, b), direct and counter impression of incomplete forewing; South Africa, Eastern Cape Province, Mount Fletcher, Tina Bridge site; Karoo basin, Upper Triassic, Molteno Formation.

Description (Figs. 1h, 1i, 2f). Medium-sized insects. Anterior margin of forewing convex, costal field three times as broad as subcostal field. SC with more than ten simple and bifurcating anterior branches, ending in distal third of the wing. R with four or five branches, dichotomizing or forming anterior crest. RS beginning around wing middle, with four to six branches, dichotomizing or forming posterior crest of branches. $M_5$ flowing into CuA proximal of its branching; median branching relatively far from base, at the level of SC apex. Median with six branches, no clear distinction between MA and MP is present. $CuA_1$ branching near its base; anterior branch of $CuA_1$ branching near middle, with two endings, directed towards wing apex; posterior branch of $CuA_1$ also two-branched, dividing somewhat more proximal than anterior branch. $CuA_2$ straight, CuP curved. Transverse veins simple, coloration patterned along them.

Measurements, mm. Length of forewing around 21–22.

Material. In addition to holotype, specimens PRE/F 15689 and 19264 from the same-age site Nieuwjaars Spruit (South Africa, Orange Free State).

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