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A NEW SPECIES OF *GLAPHYROPHLEBIA* HANDLIRSCH, 1906 (INSECTA: NEOPTERA: BLATTINOPSIDAE) FROM THE LOWER PERMIAN WELLINGTON FORMATION OF NOBLE COUNTY, OKLAHOMA, USA

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Abstract—Two species of the fossil insect genus *Glaphyrophlebia* are known from the Wellington Formation of Kansas (USA). In 1909, E. H. Sellards described *G. ovata* (Sellards, 1909) in the genus *Pursa* and *G. speciosa* (Sellards, 1909) in the genus *Sindon*. In 1966, Carpenter assigned both species to *Glaphyrophlebia* Handlirsch (1906a). *Glaphyrophlebia anderhalterorum* n. sp. is described from a specimen collected from the Wellington Formation in Noble County, Oklahoma. Most species of *Glaphyrophlebia* are known from fossil remains of forewings (often fragmentary), and occasionally hind wings. The holotype of *G. amderhalterorum* is a compression fossil comprising a nearly intact insect in dorsal aspect with articulated wings, and with portions of the hind, mid and fore-legs, thorax, and a portion of the head and abdomen preserved. This appears to be only the second glaphyrophlebiid fossil for which significant portions of body parts are preserved; a specimen of *G. uralensis* (Martynov, 1940) comprised a complete insect in lateral aspect, with body, head, legs, wings, and genitalia intact. *G. anderhalterorum* is the first species of *Glaphyrophlebia* to be described from the Oklahoma Permian.

INTRODUCTION

Handlirsch (1906a) described his new fossil insect genus *Glaphyrophlebia* in a new order, Protoblattoidea, new family Oryctoblattinidae. He characterized *Glaphyrophlebia* as having "much more reduced" venation (Handlirsch, 1906a, p. 707) than other genera he placed in the family (e.g., *Blattinopsis* Giebel, 1867). The type species was *G. pusilla* Handlirsch, 1906a, from the Pennsylvanian of Mazon Creek, Illinois.

In 1909, E. H. Sellards described two species from the Elmo, Kansas insect fossil beds that he placed in Oryctoblattinidae: *Pursa ovata* Sellards, 1909 and *Sindon speciosa* Sellards, 1909. In 1925, Bolton described the new family Blattinopsidae, to which he assigned "…a part of the Oryctoblattinidae of Handlirsch" (Bolton, 1925, p. 23). He included genus *Blattinopsis* in the family Blattinopsidae, but made no mention of *Glaphyrophlebia*, *Pursa* or *Sindon*. In her review of the family Blattinopsidae, Kukalová (1959) placed a number of genera, including *Glaphyrophlebia*, *Pursa*, *Sindon*, in the family, which she argued for placement in the order Protorthoptera. In 1966, Carpenter redescribed Sellards' species, assigning them both to *Glaphyrophlebia*.

The most recent review of family Blattinopsidae (Hörnschemeyer and Stapf, 2001) lists 13 species of *Glaphyrophlebia* from the Upper Carboniferous through the Late Permian, from North America, England, Asian and European Russia, France, Germany, and Czech Republic (species list is repeated in Appendix herein for completeness, along with references to figures of species to facilitate comparisons and diagnoses). The new species described here is the third species of the genus from the Wellington Formation, the fourth from North America, and the fourteenth overall.

METHODS

Photomicrographs of the part and counterpart were made using two systems: a Nikon 990 digital camera with an American Optical dissecting microscope and an external strobe flash (Nikon SB-26) or a Nikon D1x digital camera attached to an Infinity K-2 long-distance microscope lens and custom fiber-optic strobe illuminators. Flash orientation was optimized to show details of interest. The photographed images were processed using Adobe Photoshop 6.0 and imported into a vector-graphics software program (XARA Extreme 4.0, XARA Group, Ltd., London), where they were assembled into composite images. The venation reconstruction drawing was made as an overlay (Fig. 1), using photographs of both part and counterpart.

Interpretation and nomenclature for the wing venation follows Kukalová-Peck (1991), as amended by Kukalová-Peck & Brauckmann (1992). To facilitate comparison with species discussed in the review of the Blattinopsidae of Hörnschemeyer and Stapf (2001), we note the following correspondence:

Vein	Notation used here	Notation of Hörnschemeyer and Stapf
posterior subcosta	ScP	Sc
anterior radius	RA	R
posterior radius	RP	RS
posterior media	MP	MP
anterior cubitus	CuA	CuA
posterior cubitus	CuP	CuP
anterior analis	AA	A
vein bow	vb	vb

SYSTEMATIC PALEONTOLOGY

INSECTA
NEOPTERA
Blattinopsidae Bolton, 1925
***Glaphyrophlebia* Handlirsch, 1906a**
***Glaphyrophlebia anderhalterorum* n. sp.**
Figures 1-3

Diagnosis: The new species is assigned to family Blattinopsidae based on broad area between ScP and RA (see Fig. 1 for venational nomenclature), presence of vein bow, nearly parallel CuA and posterior branch of MP with distinct diagonal brace ("strut" of Béthoux and Nel, 2002; "arculus" of Kukalová-Peck and Brauckmann, 1992); assigned to genus *Glaphyrophlebia* on the basis of the following characters (as elucidated by Hörnschemeyer and Stapf, 2001): no reticulation in distal half of wing; only a few cross veins connecting branches of RA and MP; longitudinal furrows between branches of RA and MP running from the

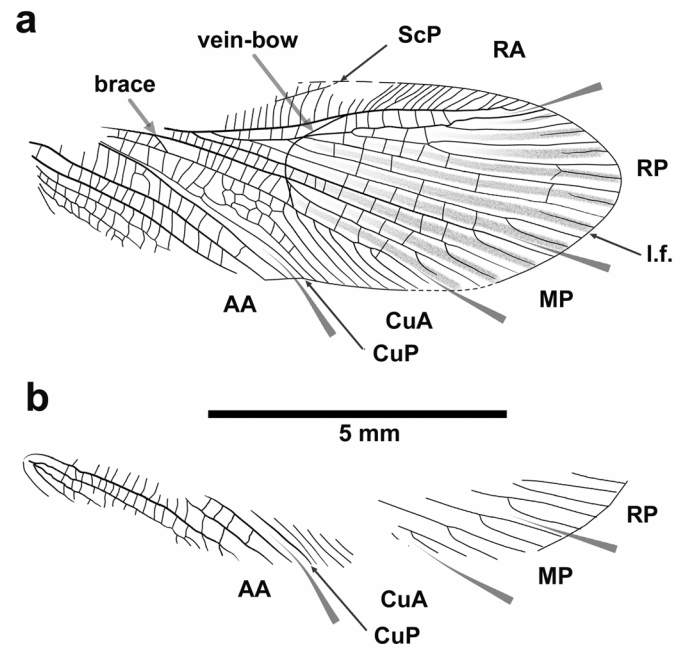

FIGURE 1. Reconstruction of forewings of *Glaphyrophlebia anderhalterorum* n. sp. **a**, Right forewing. **b**, Left forewing. Scale bar 5 mm long. ScP = posterior subcostalis; RA = anterior radius; RP = posterior radius; l.f. = longitudinal furrow (indicated by gray shading; depicted only on RFW); MP = posterior media; CuA = anterior cubitas; CuP = posterior cubitus; AA = anterior analis. Notation and interpretation of venation follows Kukalová-Peck, 1991.

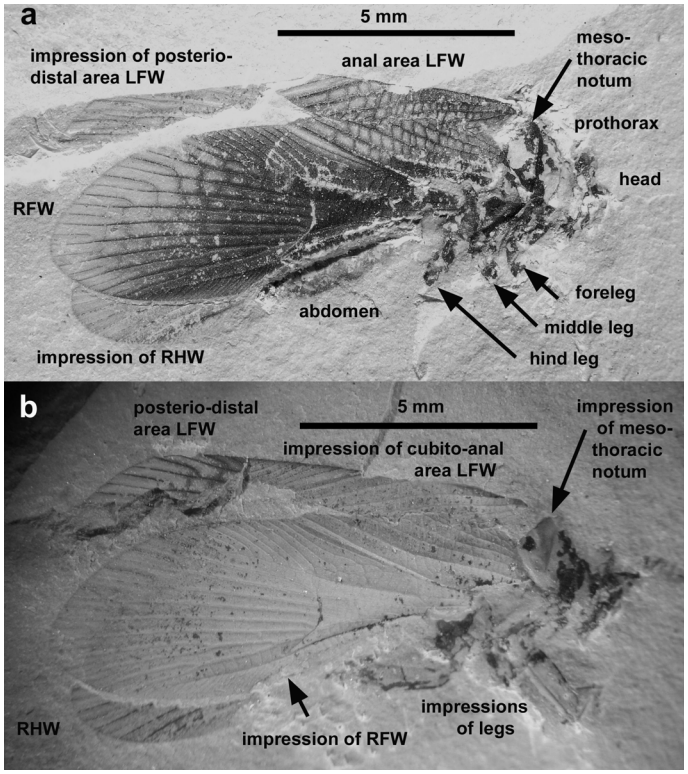

FIGURE 2. *Glaphyrophlebia anderhalterorum* n. sp. Photographs of Holotype. **a**, Part: Specimen KU-R5-4-26-04-001a. Dorso-lateral view of nearly complete insect with articulated wings and legs, showing color pattern with darkening of wing veins and of the membrane of the basal radio-medial fields, the membrane lightening in color distally. **b**, Counterpart (image digitally flipped): Specimen KU-R5-4-26-04-001b. Impression of insect. Both scale bars 5 mm. RFW = right forewing; LFW = left forewing; RHW = right hind wing.

posterior wing margin to or slightly basal of vein-bow; basal cubital field with large cells formed by a network of cross veins.

Species-level Differential Diagnosis: *Glaphyrophlebia anderhalterorum* differs from *G. arnulfi* Hörnschemeyer and Stapf, 2001 in size (FW length 10.5 mm vs. 21 mm); fewer and more widely spaced cross veins in RP field; MP with two vs. one main branch.

Differs from *G. clava* Kukalová, 1965 by closely-spaced vs. widely-spaced slanted cross veins between R and the costal margin distal of ScP termination; lack of network of cells formed by cross veins between RA and most anterior branch of RP at wing apex; simple cross veins in radial-medial field basal of vein-bow; CuP and AA1 with space between them widening towards posterior margin of wing rather than closely spaced and parallel.

Differs from *G. delicatula* Handlirsch, 1906 in fewer simple cross veins in distal Rs field; lack of cross veins between branches of RP and intercalary veins (type of *G. delicatula* comprises only the distal half of ScP and RA and the RP field, with remainder of wing missing).

Differs from *G. jeckenbachi* Hörnschemeyer and Stapf, 2001 by two main branches of MP, anterior branch single and arising from RA just basal of origin of RP, posterior branch forking at level of vein-bow rather than single branch forking distal to vein-bow; CuA with distal branches pectinate vs. CuA forking once or twice and pectinate branches arising from most posterior branch of fork; simple cross veins in medial field basal of vein-bow vs. unevenly spaced and slanted cross veins; simple and more evenly spaced cross veins in anal field vs. slanted veins and networks of veins.

Perhaps most similar to *G. ovata* (Sellards, 1909), *G. anderhalterorum* differs from that species by simple cross veins between RA and ScP basal of vein bow rather than double row of cells; width of field between RA and ScP about ½ width of field between ScP and costal margin rather than subequal at level of vein bow; two main branches of MP, anterior branch single and arising from RA just basal of origin of RP, posterior branch forking at level of vein-bow rather than single branch; CuA with distal branches pectinate vs. CuA forking at vein bow and pectinate branches arising from most posterior branch of fork; simple cross veins in cubital field near brace rather than network of cells; fewer cross veins in RP and MP fields distal to vein-bow.

Differs from *G. parvavena* Hörnschemeyer and Stapf, 2001 in vein-bow terminating on RA at level of ScP terminating on costal margin vs. vein-bow terminating on RA well distal of ScP termination; more and more uniformly-spaced cross veins in RP and MP fields; simple cross veins rather than network of cross veins between first two anal veins; general shape of longitudinal veins straight rather than sinuate or curved.

Differs from *G. pusilla* Handlirsch, 1906 by two main branches of MP, anterior branch single and arising from RA just basal of origin of RP, posterior branch forking at level of vein-bow rather than a single forked branch; simple cross veins between ScP and RA and RP and most anterior branch of RP rather than forked cross veins; CuA straight rather than sinuate.

Differs from *G. pygmaea* (Meunier, 1907) by two main branches of MP, anterior branch single and arising from RA just basal of origin of RP, posterior branch forking at level of vein-bow rather than free MP with 4 anteriorly pectinate branches.

Differs from *G. rohwedderi* Hörnschemeyer and Stapf, 2001in total forewing length 10.5 mm vs. 15.8-16.5 mm, width 3.7 mm vs. 6.4-6.7 mm; CuA with distal branches pectinate vs. CuA forking once or twice and pectinate branches arising from most posterior branch of fork; large cells vs. irregular mesh of cells between CuA and CuP; simple cross veins vs. network of cells between anal veins basally, few widely-spaced cross veins vs. dense system of cross veins in RP and MP fields.

Differs from *G. speciosa* (Sellards, 1909) by more closely spaced

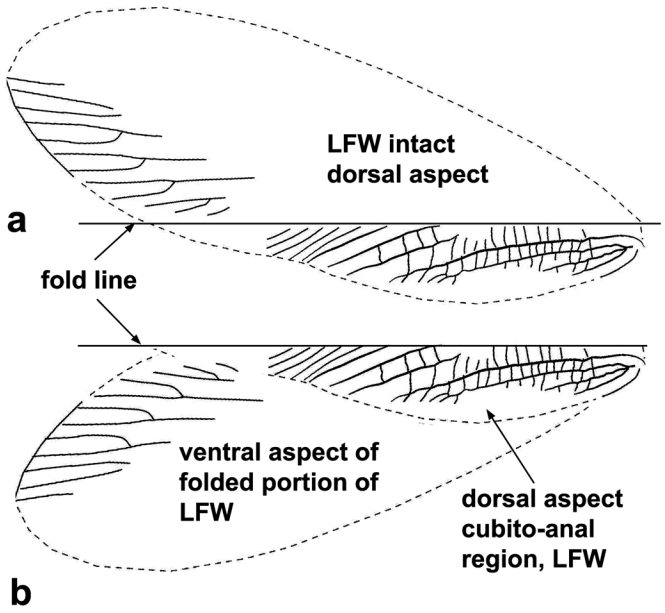

FIGURE 3. Drawing depicting likely geometry of the folding under of the left forewing (LFW) of the insect during preservation. The wing may have simply folded, or may have broken off; the arrangement of preserved portions suggests that the wing folded ventrally along a line running through the cubital field. **a**, The preserved portions of the left forewing presented as they would have appeared on the intact wing, with the supposed fold line indicated. **b**, The wing as preserved, reflecting result of the ventral folding.

slanted cross veins between RA and costal margin distal of ScP termination; vein-bow terminating on RA at level of vs. distal to ScP termination; two main branches of MP, anterior branch single and arising from RA just basal of origin of RP, posterior branch forking at level of vein-bow rather than MP free and unforked; pectinate branches of CuA closely spaced and parallel vs. widely spaced and curved, branches of CuA more nearly parallel to anterior branch; simple cross veins rather than network of cells between anal veins basally.

Differs from *G. subcostalis* (Martynov, 1928) by two main branches of MP, anterior branch single and arising from RA just basal of origin of RP, posterior branch forking at level of vein-bow rather than MP free and unforked; CuA with distal branches pectinate vs. CuA forking and pectinate branches arising from posterior branch of fork; simple cross veins vs. network of cells between anal veins basally.

Differs from *G. uralensis* (Martynov, 1940) by posterior branch of MP straight and forked at level of vein-bow vs. curved and simple; CuA straight vs. curved; pectinate branches of CuA parallel and simple vs. unevenly spaced and sometimes separated from main branch by irregular cells.

Differs from *G. wettinensis* (K. v. Fritsch, 1899) by more closely spaced slanted cross veins between RA and costal margin distal of ScP termination; posterior branch of MP straight and forked at level of vein-bow vs. posterior branch forking twice, fork basal to vein-bow, second fork on posterior branch of first fork; pectinate branches of CuA straight, parallel and simple vs. curved or branched, unevenly spaced and separated from main branch by irregular cells.

Differs from possible *Glaphyrophlebia* (gen. et sp. indet. Prokop et al., 2012: p. 279, figs. 7, 8) by short versus long stem of RP; simple cross veins vs network of cells between MP and CuA basal to brace vein; fewer and more widely spaced cross veins in radial and medial fields.

Etymology: The specific epithet *anderhalterorum* honors my maternal grandmother, the late Katherine Vollet Anderhalter, and her son, the late Prof. Dr. Oliver Anderhalter. My grandmother encouraged me from my earliest school days to excel academically so that I might follow in my uncle's footsteps and earn a PhD. Her expectations and his example nurtured in me an early interest in science and learning that has lasted a lifetime.

Type Locality: Raasch 5 locality (Raasch, 1946), Noble County, Oklahoma, USA; Wellington Formation, Artinskian, Lower Permian.

Type Material: Holotype specimen KU-R5-4-26-04-001a,b. Collected in April, 2004 by Joseph Hall of Tulsa, Oklahoma, and provided to the author for contribution to the Fossil Insect Collection, Entomology Division (Paleoentomology) of the University of Kansas Natural History Museum.

Part (001a, Figure 2a): Well-preserved insect exposed in dorsal aspect, with some rotation about the lengthwise body axis to expose portion of right side; wings articulated to pterothorax; significant three-dimensionality of body and wing venation intact; dorsal surface of entire right forewing (RFW) nearly complete, but with subcostal region and extreme anterio-basal portion missing; impression of anterio-distal portion of right hind wing (RHW) visible because of rotation of body; anal area of LFW preserved, but LFW apparently folded ventrally along a line through the cubital area (see Fig. 3), leaving an impression of the posterio-distal portion of the ventral LFW; right legs articulated, each with portion of leg distal to approximately mid-femur obscured; meso-thoracic notum with triangular shaped and rounded bulge above level of wings; prothoracic tergum and fragments of head visible; antennae missing or obscured; ventral portion of abdomen visible, terminalia missing or obscured.

Counterpart (001b, Figure 2b): Clear and detailed impression of dorsal aspect of insect revealing some portions of wing venation of both LFW and RFW not visible in part; portion of ventral surface of posterio-distal portion of folded LFW preserved; impressions of legs with more distal portion of femur preserved, especially in foreleg, for which nearly the entire femur appears to be impressed; three-dimensionality of mesothoracic notum particularly noticeable in impression.

Description: Forewing (Fig. 1a, b): Preserved length 10.3 mm, estimated total length 10.5 mm, width 3.5 mm, ratio length to width: 3.0; except for sinuate RA, longitudinal veins and branches straight and evenly spaced, often parallel to a marked degree; ScP terminates at 5.5 mm from wing base (at mid-wing), closely-spaced, slanted simple or y-shaped cross veins between RA and costal margin distal to ScP termination, cross veins between RA and ScP more widely spaced and simple; at level of vein bow, field between RA and ScP ½ the width of field between ScP and costal margin; RA sinuate and terminating 8.7 mm from base, RP separating from RA at 3.4 mm from wing base, forking 5 times, with few cross veins between longitudinal branches of RP; MP with two straight branches, anterior branch separating from RA 3.1 mm from wing base, posterior branch forking at level of vein-bow; longitudinal furrows between branches of RP and MP, extending from margin of wing to vein-bow; CuA separates from MP+CuA 2.4 mm from wing base; CuA straight, with 9 branches terminating on wing margin, closely spaced and pectinate, some large cells in CuA field basal to vein bow, simple cross veins between CuA and CuP basal to these cells; CuA and anterior branch of A not parallel, distance wider at wing margin than basally, sharp fold line between CuP and A; at least six parallel anal vein branches with simple cross veins, lacking network of cells; cross veins in RP/MP field distal of vein-bow few and widely separated; vein bow definitely and distinctly vein-like, extending from RA at the level of ScP termination, curving basally, terminating on CuA 4.8 mm from wing base; wing veins and membrane in basal 2/3 of wing distal to anal region darkened; width of thorax between forewing attach points 1.8 mm.

Thorax: Mesothorax with triangular-shaped, dorsally-rounded tergum, 1.8 mm wide, 1 mm long; prothoracic tergum 1 mm wide by 0.8 mm long.

Abdomen: Short, apparently three terminal segments and possibly extreme basal portion of terminalia (latter indistinct) preserved; approximately 4 mm preserved length; forewing extends 4 mm beyond abdomen.

Discussion: The type specimen of *Glaphyrophlebia anderhalterorum* n. sp. has extremely well-preserved venation, and the vein-bow, viewed by some authors as possibly an impressed mark (e.g., Bolton, 1925; Kukalova, 1959), is definitely present here as a strong vein, as strong as the longitudinal veins it crosses, supporting the assertion of Hörnschemeyer and Stapf (2001) that it likely plays a role in stiffening the wing basal to the vein-bow while allowing flexing of the distal surface.

In the differential diagnosis (vide supra) I have chosen to take note of differences in the branching of MP, even though that vein system is known to be highly variable in the Blattinopsidae; in each case, there are other significant differences supporting the specific identity of *G. anderhalterorum*.

Specimens of Blattinopsidae from the Wellington Formation are not abundant, although the Elmo species, *G. ovata* and *G. speciosa*, are represented by at least several specimens each from Kansas, and the author has also seen small numbers of specimens of *G. speciosa* from the Noble County, Oklahoma beds. Thus far only one specimen of *G. anderhalterorum* has been found. As noted by Beckemeyer and Hall (2007), from data based on a set of 120 species of insects known from the Elmo, Kansas fossil beds, the mean number of specimens per species was 21, the median 2 and the mode 1, verifying that most of the Elmo species are known from a single specimen.

According to Hörnschemeyer (1998), only 56 fossils of Blattinopsidae had been mentioned in the literature prior to the discovery of about 100 specimens from the Lower Permian Niedermoschel fossil site. The unusual numerical abundance of blattinopsiid fossils at Niedermoschel resulted in the addition of four species from that locality to the genus *Glaphyrophlebia*. It is interesting that although *Glaphyrophlebia* specimens are much less abundant in the Wellington Formation, there are now three species known.

As noted by Hall (2004) and Beckemeyer (2011) the Oklahoma Wellington Formation insect deposit facies are derived from marginal marine lagoon sediments, with insect remains likely comprised of allochthonous material washed in by streams. This undoubtedly accounts for the preponderance of fossils from the deposits being comprised of wings and wing fragments. The preservation of this fine example of a nearly complete glaphyrophlebiid is thus unusual; hopefully, continued collection from the Wellington Formation beds will provide additional such surprises.

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Mr. Joseph Hall, of Tulsa, Oklahoma has been my field companion and fellow collector for a number of years. He has always generously parted with even the most exceptional specimens in the interest of the advancement of science. Prof. Dr. Michael Engel supports my work through affiliation with his Paleoentomology Laboratory at the University of Kansas Natural History Museum, Division of Entomology (Lawrence, Kansas). Ms. Betty Sherwood of the Wichita State University Inter-Library Loan department (Wichita, Kansas) provided timely access to many difficult-to-find references. Dr. Danil Aristov of the Paleontological Institute of the Russian Academy of Sciences (Moscow) provided a critical reference not otherwise available. Drs. Michael Engel and Jakup Prokop (Faculty of Science, Department of Zoology, Charles University, Prague) provided comments on an earlier version of this manuscript. The work reported here is a contribution of the University of Kansas Natural History Museum, Division of Entomology.

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APPENDIX

Species of *Glaphyrophlebia* with References to Reconstruction Figures or Photographs (Species list after Hörnschemeyer & Stapf, 2001)

Glaphyrophlebia Handlirsch, 1906a

- *G. anderhalterorum* n. sp.
  [Figs. 1 (reconstruction drawing), 2 (photograph) and 3 (reconstruction drawing) herein]
- *G. arulfi* Hörnschemeyer & Stapf, 2001
  [p. 99-100, fig. 12: reconstruction]
- *G. clava* Kukalová, 1965
  [p. 85, fig. 14: reconstruction, pl. 7: fig. 2: photograph of FW]
- *G. delicatula* Bolton, 1934
  [p. 284, fig. 5: reconstruction, pl. 9: fig. 5: photograph of FW]
- *G. jeckenbachi* Hörnschemeyer & Stapf, 2001
  [p. 95-97, figs. 8: reconstruction, fig. 9: photograph]
- *G. ovata* (Sellards, 1909) (Pursa)
  [p. 155, fig. 4: reconstruction; Carpenter, 1966, p. 71, fig. 9: reconstruction of neotype]
- *G. paravena* Hörnschemeyer & Stapf, 2001
  [p. 100-101, fig. 13: reconstruction]
- *G. pusilla* Handlirsch, 1906a
  [p. 707: fig. 35: reconstruction of type species for genus; Handlirsch, 1906b, pl. 16, fig. 10: reconstruction]
- *G. pygmaea* (Meunier, 1907) (Blattinopsiella)
  [p. 524: fig. 2: reconstruction; Hörnschemeyer and Stapf, 2001, p. 89, fig. 2: photograph of wings]
- *G. rohwedderi* Hörnschemeyer & Stapf, 2001
  [p. 98, fig. 10, p. 99, fig. 11: reconstructions]
- *G. speciosa* (Sellards, 1909) (Sindon)
  [p. 155, fig. 1: reconstruction; Carpenter, 1966, p. 70, fig. 8: reconstruction of neotype; Carpenter, 1992, p. 104, fig. 59.9: reconstruction of neotype]
- *G. subcostalis* (Martynov, 1928) (Sindonopsis)
  [pl. 12, fig. 3, FW; pl. 7, fig. 7, HW (as *Sindonopsis reducta*); Martynov, 1931 (as Sindon rossicum), p. 154, fig. 4; Sharov, 1962, p. 116, fig. 277: reconstruction of HW; Rasnitsyn, 1980, p. 32, fig. 29a: reconstruction of FW, fig. 29b: reconstruction of HW; Novokshonov, 1998, p. 30, fig. 6: reconstruction of complete insect in lateral view; Rasnitsyn and Quicke, 2002 (p. 108, fig. 110: photograph of FW and HW)]
- *G. uralensis* (Martynov, 1940) (Sindon)
  [(p. 14, text fig. 9, plate II, fig. 4); Sharov, 1962, p. 116, fig. 276: reconstruction of FW; Rasnitsyn, 1980, p. 32, fig. 28a: reconstruction of complete insect in lateral view, p. 32, fig. 28b: artist's conception of living insect; Rasnitsyn and Quicke, 2002 (p. 108, fig. 110: photograph of complete insect in lateral view)]
- *G. wettinenesis* (K. v. Fritsch, 1899) (Prisca)
  [v. Fritsch does not figure P. wettinensis; Handlirsch, 1906b, pl. 6, fig. 12: reconstruction; Hörnschemeyer & Stapf, 2001, p. 91, fig. 3: reconstruction after Handlirsch, 1906b]

gen. et sp. indet. (likely glaphyrophlebiid) (Prokop et al., 2012)
[p. 289, figs. 7,8]