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Upper Carboniferous Insects from the Pottsville Formation of Northern Alabama (Insecta: Ephemeropterida, Palaeodictyopterida, Odonatoptera)

By

Roy J. Beckemeyer [1,2] and Michael S. Engel[1,3]

1 Division of Entomology (Paleoentomology), Natural History Museum, Biodiversity Institute, and Department of Ecology and Evolutionary Biology, 1501 Crestline Drive – Suite 140, University of Kansas, Lawrence, Kansas 66045;
E-mail: (RJB) royjbeckemeyer@cox.net; (MSE) msengel@ku.edu
2 957 Perry Ave., Wichita, Kansas 67203-3141
3 Corresponding author

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ABSTRACT New Upper Carboniferous (Pennsylvanian, Westphalian A) insects are described from localities in the Pottsville Formation of northern Alabama (including the Union Chapel Mine). Five species are recorded in five palaeopterous orders and comprising five genera (four new to Science). New taxa proposed are: *Anniedarwinia alabamensis* new genus and species (Ephemeropterida: Syntonopterodea: Syntonopteridae); *Pharciphyzelus lacefieldi* new genus and species (Palaeodictyopterida: Palaeodictyoptera: Homoiopteridae), *Camptodiapha atkinsoni* new genus and species (Palaeodictyopterida: Diaphanopterodea: Namurodiaphidae); *Agaeoleptoptera uniotempla* new genus and species (Palaeodictyopterida: Megasecoptera: Ancopteridae); and *Oligotypus tuscaloosae* new species (Odonatoptera: Protodonata: Paralogidae). Each taxon is described, figured, and compared with close relatives in Carboniferous and Permian deposits. *Camptodiapha* new genus extends the geographical range of the family Namurodiaphidae into the Carboniferous of North America. The diagnosis of the family Ancopteridae is expanded to accommodate *Agaeoleptoptera* new genus rather than propose another monogeneric family. The distribution of Ancopteridae is extended geographically into North America and temporally into the Upper Carboniferous. A key to the genera of ancopterids is provided.

KEY WORDS: Alabama; taxonomy; Pennsylvanian; Syntonopterodea; Syntonopteridae; Ephemeroptera; Palaeodictyoptera; Lycocercidae; Diaphanopterodea; Namurodiaphidae; Megsecoptera; Ancopteridae; Protodonata; Paralogidae.

INTRODUCTION

The Carboniferous insect fauna of North America has received considerable attention since the initial studies by Scudder and his contemporaries on deposits in Illinois, Pennsylvania, Rhode Island, Kansas, Massachusetts, and the Maritime Provinces of Canada (e.g., Scudder, 1868a, 1868b, 1868c, 1878, 1879, 1885a, 1885b, 1893, 1895; Dana, 1864; Sellards, 1904; Handlirsch, 1906a, 1911, 1919). Subsequently, Carpenter and Kukalová-Peck, among others, provided a series of contributions extensively revising and further documenting the Carboniferous insect fauna (e.g., Carpenter, 1933, 1938, 1940, 1960, 1963b, 1964, 1965, 1967, 1980, 1983, 1987, 1992a, 1992b, 1997; Carpenter and Richardson, 1968, 1971, 1976; Richardson, 1956; Copeland, 1957; Kukalová-Peck, 1987, 1997a; Kukalová-Peck and Richardson, 1983; Burnham, 1983; Béthoux, 2006, 2007, 2008, 2009; Béthoux and Briggs, 2008: vide etiam Béthoux et al., 2008, for consideration of Kukalová-Peck's hypotheses). Supplementing these more comprehensive works have been various isolated records from deposits in Utah, Missouri, Tennessee, New Mexico, Ohio, and Kentucky (e.g., Carpenter, 1967, 1970; Lewis, 1979; Nelson and Tidwell, 1987; McComas and Mapes, 1988; Brauckmann et al., 1993; Rasnitsyn et al., 2004). Outside of these, work on the Carboniferous of North America has slowed in recent decades and new deposits bearing insects have not been forthcoming. However, recent collecting in the Upper Carboniferous Pottsville Formation, primarily at the Union Chapel Mine in north-central Alabama, has uncovered insect material, albeit uncommonly (Lacefield, 2000; Atkinson, 2005). Although represented entirely as fragments of wings, these compressions are exceptionally well preserved and document a similar breadth of ordinal diversity already well known from similar-aged deposits elsewhere in North America and Europe.

Herein we provide a preliminary account of the insect diversity based on five well preserved insect wings recovered over the course of several years from the Pottsville Formation. The McWane Science Center has an additional insect comprised of the apex of a small wing (very roughly estimated to be the distal 15–20%). No catalogue or accession number was assigned to the specimen, although it was accompanied by a paper label with the annotations: "Object: dragonfly wing / UCM No. [blank] / Horizon: Pottsville Fm. / Locality: UCM / Collected by: Prescott Atkinson / Date: 2008." Despite the label attribution of "dragonfly", the preserved portion (approximately 8 by 14 mm) is too incomplete to allow definite taxonomic assignment of this fossil at either familial or ordinal level. This specimen and those described herein make up the only insect fossils, other than ichnofossils, currently known from the Pottsville Formation of Alabama. The University of Kansas is mounting an excavation in the hopes of more fully documenting the insect fauna of the Pottsville Formation.

ACKNOWLEDGMENTS

We extend our thanks to Dr. Prescott Atkinson, who, in his role as Vice President of the Alabama Paleontological Society (APS) and Project Manager for the Union Chapel Mine (UCM), invited our review and study of these fossils. He also generously provided lodging and local transportation for the authors' respective visits, and made arrangements with the museums for making the specimens and working space available. Dr. Atkinson and the APS were instrumental in campaigning for the preservation of the UCM locality, now known formally as the Steven C. Minkin Paleozoic Footprint Site, a holding of the Alabama Department of Conservation and Natural Resources (ADCNR). The State Lands Division of ADCNR is acknowledged for taking the Union Chapel Mine site under their protection and thereby making possible the future recovery of such specimens as those described in this paper. Prescott Atkinson and Milo Washington, APS Field Trip Coordinator, also hosted the authors on field trips to the UCM locality. Dr. Randy Mecredy, Director, and Michael Dressler, Collections Assistant, of the Alabama Museum of Natural History, and Mr. Jun Ebersole, Collections Manager at the McWane Science Center, were all very supportive and helpful. They provided first class working space and equipment, and thereby made the time spent in their facilities efficient, productive, and pleasant. The hospitality and professionalism of all the above are sincerely appreciated. In the initial stages of identifying several of these fossil wings, the character list and character matrix of Prokop and Ren (2007), were quite helpful. Lastly, we are grateful to the efforts of Dr. Carsten Brauckmann, Dr. Jakub Prokop, Dr. Jörg Schneider, and Dr. Kirsten Jensen, the last as editor, for constructive input and important contributions that significantly improved the manuscript. Financial support was provided by U.S. National Science Foundation grant DEB-0542909 (to MSE). This is a contribution of the University of Kansas Natural History Museum Entomology Division (Paleoentomology).

MATERIALS AND METHODS

Geological Setting

The insect fossils described in this paper were collected from the Early Pennsylvanian (Westphalian A) Pottsville Formation, Mary Lee coal zone, in northern Alabama from localities associated with strip mines. All the sites are in the Black Warrior coal basin (Murrie et al., 1976); two are in Walker County and one in Tuscaloosa County (Fig. 1). Most of the fossils are from the former Union Chapel Mine in Walker County, a reclaimed mine site now preserved as the Steven C. Minkin Paleozoic Footprint Site, a Carboniferous plant and ichnofossil (invertebrate and vertebrate trackway) lagerstätte known for producing large numbers of high quality fossils (Buta et al., 2005). The mine covers parts of the eastern half of sec. 21 and the western half of sec. 22, T. 14S, R. 6W, in the Cordova 7.5-minute topographic quadrangle (Pashin, 2005). As the fossils are found in overburden spoils, the exact stratigraphic position of their origin is not always determinable. The generalized stratigraphic section shown in Fig. 1 (after Pashin, 2005) shows that the shales in the alternating shale-sandstone sequences below and above the Mary Lee coal beds are the source of the terrestrial plant and trackway fossils. The three Union Chapel Mine specimens were all found between 2000 and 2008; two are associated with plant materials, one with tetrapod trackways.

One of the fossil insect specimens was found in 1988 in a spoil pile associated with an unidentified strip mine at Windham Springs, Tuscaloosa County. More specific location information for this site is not available. Another was collected in 1993 at an open pit coal mine "approximately 100 yards east of Alabama Highway 13, approximately 2 miles north of Eldridge in Walker County" (Lacefield, pers. comm., 2010) (Sec. 5, T. 13S, R. 10W). According to Lacefield, the mine was operated by the Haley Brothers and Barbour Coal Company, with head offices in Haleyville, Alabama. It has since been reclaimed and the site is now part of the right-of-way for a four-lane highway. This specimen came from "a shale sequence of the Pottsville Formation, possibly an interval between the Jagger coal seam and the Mary Lee coal" (Lacefield, pers. comm., 2010).

Methods

All specimens were photographed with a digital macro camera (Casio Exilim EX-FH20) and all except UCM2368 and 2369 were scanned at 1200–2400 pixel-per-inch resolution using a Hewlett-Packard flat bed scanner. In addition, photomicrographs using a Nikon 990 digital camera with external strobe flash (Nikon SB-26) were made of most of the specimens to provide venation details. Flash orientation was optimized to show details of interest. Image processing software (Adobe Photoshop 6.0, Adobe Illustrator 10, and XARA Extreme 4.0.4966DL) was used to overlay images as required to produce the final reconstruction drawings of wing shape and venation. Final photographic images for the figures presented here are for light sources from the top left. The classification followed is generally that of Grimaldi and Engel (2005) except as noted.

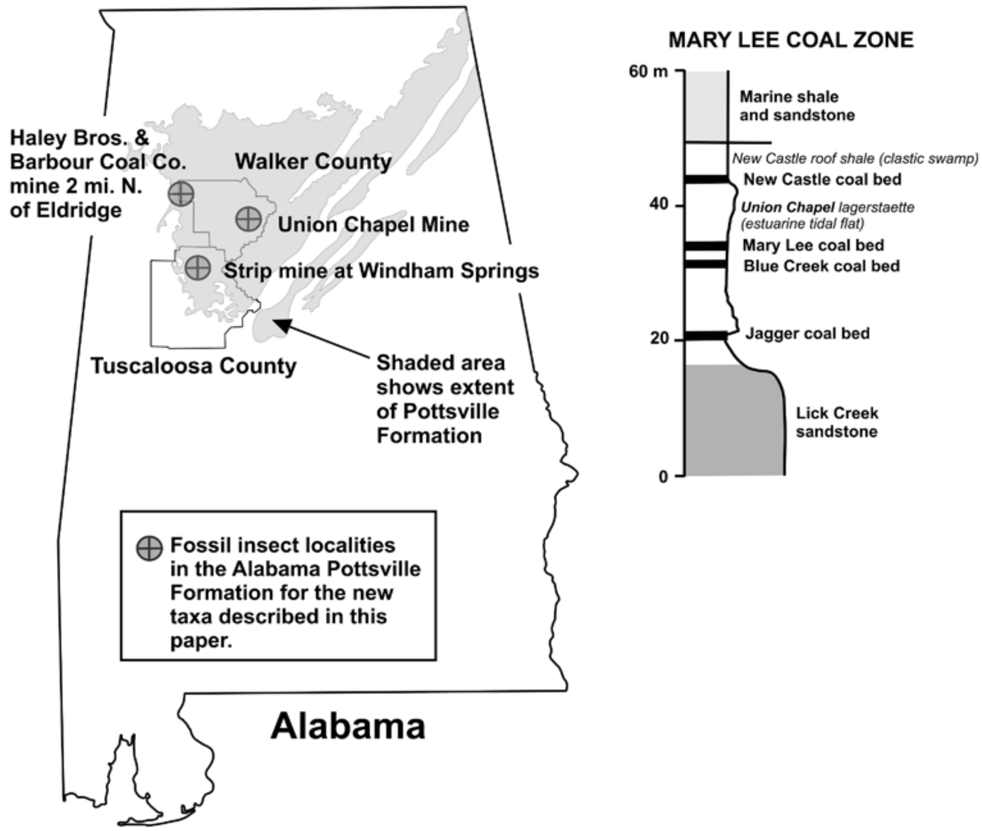

Fig. 1. Occurrence of northern Alabama Pottsville Formation fossil insects and a generalized geologic section (after Pashin, 2005) of the Early Pennsylvanian Pottsville Formation Mary Lee coal zone. Outlines of Walker and Tuscaloosa counties indicated; circular symbols mark the locations of the three sites from which fossils were collected while the shaded area indicates the extent of the Pottsville Formation in Alabama.

SYSTEMATIC PALEONTOLOGY

Superorder Ephemeropterida Pearse, 1947

Herein we use Ephemeropterida in the sense of including Syntonopterodea (Syntonopteridae), Permoplectoptera (Protereismatidae), and Ephemeroptera, but not Triplosoboptera (Triplosobidae) as its affinities with Palaeodictyopterida, or as a node between Ephemeropterida and Palaeodictyopterida, are becoming increasingly clear (e.g., Prokop and Nel, 2009).

Order SYNTONOPTERODEA Laurentiaux, 1953
Family SYNTONOPTERIDAE Handlirsch, 1911

Anniedarwinia new genus

Type species.—*Anniedarwinia alabamensis* Beckemeyer and Engel new species.

Diagnosis.—Wings [First interpreted as a fore and hind wing pair, the fossil actually comprises right and left forewings with one wing folded over the other] lacking archedictyon; origins of longitudinal veins unknown (approximately basal 30% of right forewing and basal 20% of left forewing missing); ScP terminates on costal margin approximately one-quarter wing length basad apex; RA unbranched; RP forking beyond midwing; hind wing RA and MP briefly contiguous (but not fusing) basad one-quarter wing length; MA forking basad midwing, MP forking distad to MA fork; CuA forking one-third wing length; CuP unbranched (Fig. 2); left forewing CuP and AA1 in contact at one-fifth wing length; anteriormost branch AA terminating on posterior margin near midwing; intercalary veins between terminal branches of longitudinal veins, especially numerous near wing apex.

Etymology.—The new genus-group name honors Charles Darwin's humanity by remembering his second child and youngest daughter, Anne Elizabeth "Annie" Darwin (1841–1851). Darwin nursed his ten-year-old daughter through the final stages of her illness. Her

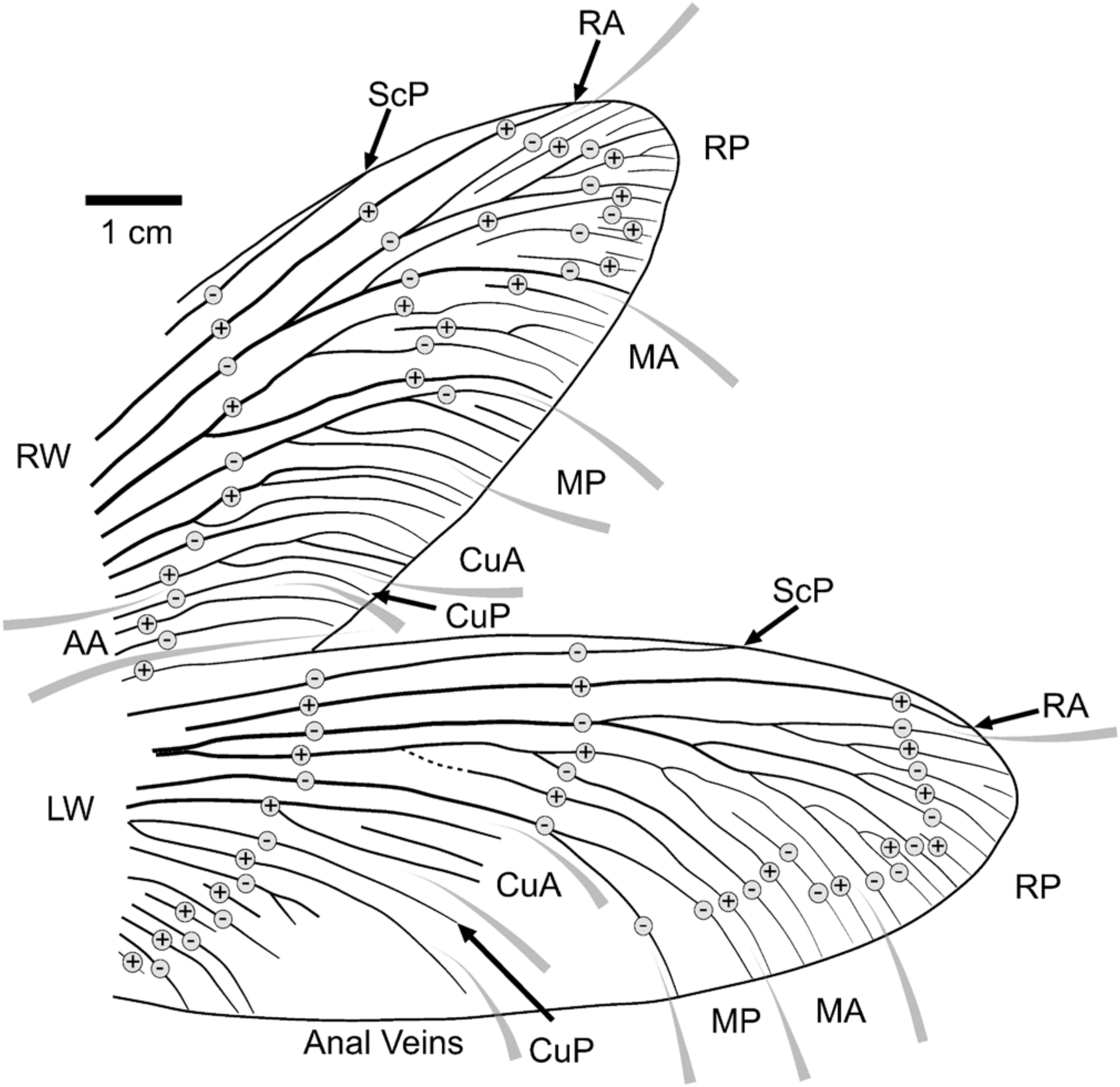

Fig. 2. *Anniedarwinia alabamensis* new genus and species (Syntonopterodea: Syntonopteridae). Reconstruction of venation of left and right forewings of holotype (UCM 1076a); veins identified and convexity (+) or concavity (–) (wing in dorsal aspect) noted.

death broke her father's heart: "We have lost the joy of our household, and the solace of our old age: she must have known how we loved her; oh that she could know now how deeply, how tenderly we do still..." (Charles Darwin, 30 April 1851: Keynes, 2001).

Discussion.—*Anniedarwinia* is much more slender than *Lithoneura* Carpenter, 1938, the only other genus for which a nearly complete wing is available (length to width ratios of 2.4 for *L. mirifica* Carpenter, 1944 hind wing, 3.0 for *A. alabamensis* new species right forewing, 2.9 for *A. alabamensis* new species left forewing). The only syntonopterid for which portions of both fore and hind wings are known is *Lithoneura lameerei* Carpenter, 1938, for which the basal third to half of the wings are preserved. In that species, the base of the hind wing is quite wide and the wing sharply tapered distally; moreover, the costal margin is much more narrow so that the hind wing shape departs significantly from the overall oval shape of the forewing. In *L. mirifica*, however, the hind wing is not significantly widened at the base and is elliptical in shape, approaching the shape of the known forewings. Thus it is difficult to allocate significance to the difference in slenderness between the forewing of *A. alabamensis* new species and the hind wing of *L. mirifica*. Moreover, MA is not fused with RP in the left forewing of *A. alabamensis* new species, instead clearly abutting it for a brief distance before diverging, while these veins fuse for a short distance in *Lithoneura*. Finally, CuP is curved posteriorly in *Lithoneura*, while this vein is straight in *Anniedarwinia*. This latter trait is more similar to *Anglolithoneura* Prokop, Nel, and Tenny, 2010, from which *Anniedarwinia* differs in the anal veins apparently not zigzagged (zigzagged in *Anglolithoneura*) and ScP and RA more widely spaced (more closely positioned in *Anglolithoneura*) (Prokop et al., 2010) (Figs. 2–4). Like all of these taxa, *Anniedarwinia* has a corrugate wing lacking an archedictyon, has CuP simple, has MA with an anterior curve such that it runs along or fuses with RP for a short distance, and has AA1 touching CuP at one point (Fig. 2). From *Gallolithoneura* Garrouste, Nel, and Gand, 2009, *Anniedarwinia* differs by the forking of MA prior to the forking of RP in both wings, the fork of MP much more strongly distad the fork of CuA (distad but relatively close in *Gallolithoneura*), the latter vein forking much more basad than in *Gallolithoneura* (Garrouste et al., 2009).

Anniedarwinia alabamensis new species
Figs. 2–4

Ephemeroptera sp.; Atkinson, 2005: 171–173, fig. 1A, 1B, 2.

Diagnosis.—As for the genus (*vide supra*).

Description.—Both wings. ScP, RA, RP, and anterior branch of MA straight, parallel and equally spaced roughly 3 mm apart at midwing; true veins and intercalary veins fairly uniformly spaced along posterio-distal margins of wing; no crossveins preserved (Figs. 2–4). Right forewing. Distal 70% of wing, preserved length 79.9 mm, preserved width 37.8 mm, estimated total wing length 114 mm; ScP terminating just basal of three-quarters of wing length; RA unbranched, terminating at 95% of wing length; RP branches at 60% wing length, RP with five branches, numerous intercalary veins, branches terminating in distal 15% of wing length; MA forking just basal to 50% wing length, MA with three branches, anterior branch running parallel to posterior branch of RP until just distal of 65% wing length, then turning rather sharply toward posterior margin, terminating just basal to 85% wing length; MP forking between 45–50% wing length; CuA forking near 35% wing length; CuP terminating just basal to 60% wing length; anal veins terminating in basal half of wing; intercalary veins numerous along posterior margin and apex of wing. Left forewing. Distal 80% of wing, preserved length 95.4 mm, preserved width 39.9 mm, estimated total wing length 115 mm; ScP terminating basal to three-quarters wing length; RA unbranched, terminating just distal to 95% of wing length; RP branching at two-thirds wing length, 6-branched, with numerous intercalary veins, branching terminating in distal 10% of wing; basal 3 mm of preserved portion of RP and MA contiguous, separating at 25% of wing length; MP forking basal to 60% wing length, 3-branched, branches terminating basal to 75% of wing length; CuA forking at one-third wing length, portion of CuA beyond 50% wing length not preserved; CuP unbranched, terminating on posterior margin at 55% wing length, most anterior anal vein in contact at 20% wing length; posterior portions of wing missing from one- to two-thirds wing length; numerous anal veins, terminating basal to 50% wing length; numerous intercalary veins at posterior margin of wing in distal one-quarter of wing; left forewing maximum width between 30 and 50% wing length, right forewing about 6% wider than left forewing (although the difference in width could conceivably be representative of the actual insect, it could also be the result of taphonomic effects).

Holotype.—PV2005.7.2.252.1 (UCM 1076a-part)/2005.7.2.252.2 (UCM 1076b-counterpart) (Figs. 3, 4), University of Alabama Museum of Natural History, Tuscaloosa, Alabama; nearly complete forewing pair with one folded over the other; basal 20–30% of wings missing; Pottsville Formation (Pennsylvanian), Union Chapel Mine, Walker County, Alabama, July 2000, T.P. Atkinson collector.

Etymology.—The specific epithet is taken from the State of Alabama, from which the type material originates.

SUPERORDER PALAEODICTYOPTERIDA PEARSE, 1936
(=ROSTRAPALAEOPTERA WOOTTON AND KUKALOVÁ-PECK, 2000)

Order PALAEODICTYOPTERA Goldenberg, 1877
Family HOMOIOPTERIDAE Handlirsch, 1906b

Pharciphyzelus new genus

Type species.—*Pharciphyzelus lacefieldi* Beckemeyer and Engel new species.

Diagnosis.—Forewing (based on the expanded area between ScP and the costal margin in the basal half of the wing) with R, M, and Cu all branching in basal third of wing and ScP extending beyond midwing (incompletely preserved but based on coarse and position ScP likely extends nearly to wing apex); pronounced bend in stems of main veins near base; R branching just distad

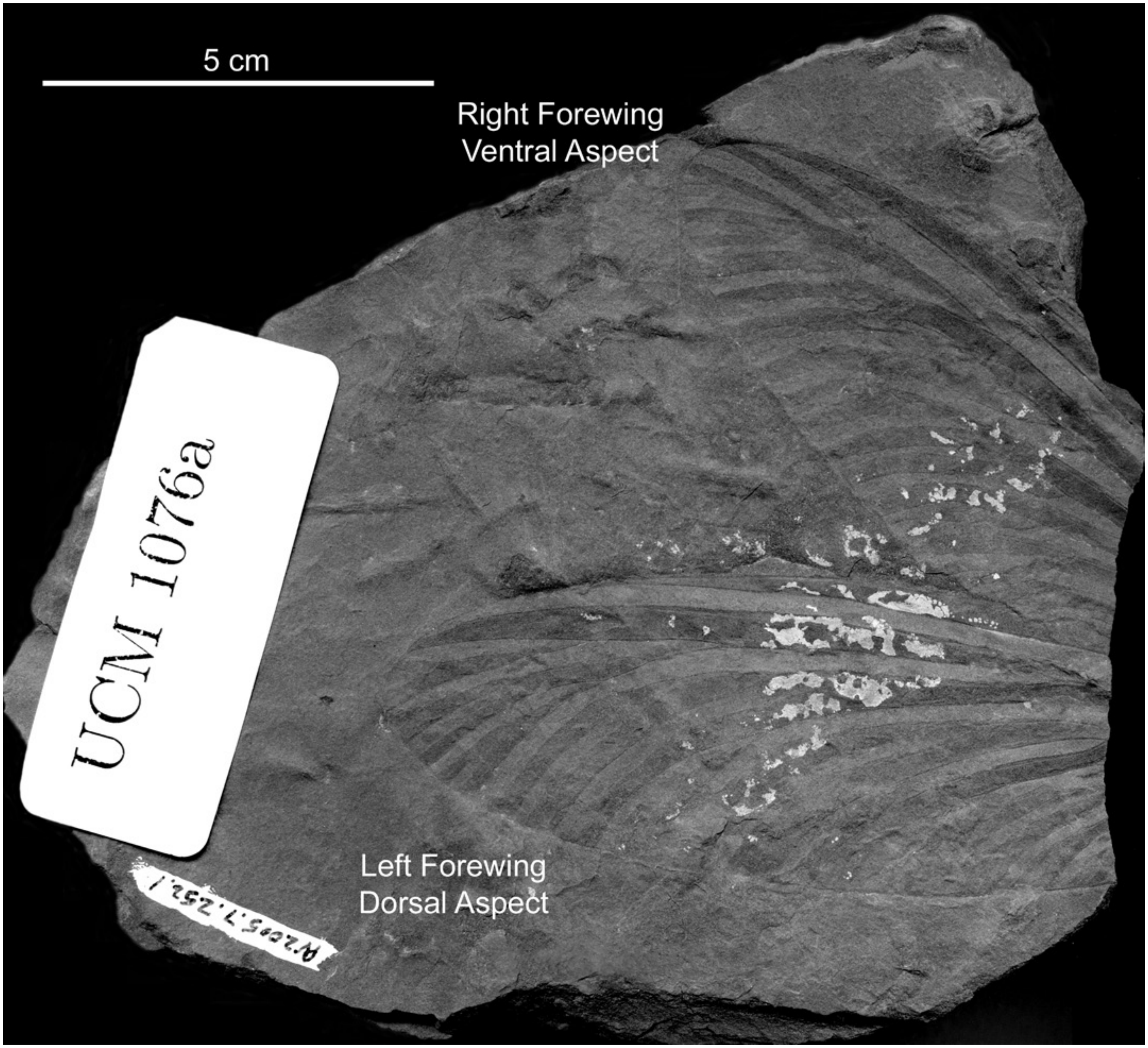

Fig. 3. Photomicrograph of holotype (UCM 1076a, part) of *Anniedarwinia alabamensis* new genus and species (Syntonopterodea: Syntonopteridae) (PV2005.7.2.252.1).

branching of M (Fig. 5A); RP branching beyond wing midlength (Fig. 5A); MA unbranched, origin of MA near and basad first branch of MP; MP area triangular and multibranched; CuA unbranched; CuP branched, CuA and anterior branch of CuP convergent at posterior margin of wing (Fig. 5A); convex ridge in wing membrane at base of anal veins forming an anal brace; crossveins very numerous and mostly reticulate (Fig. 5) (some crossveins anastomosing but not reticulate as in true Breyeriidae Handlirsch, 1906b, contra tentative identification in Atkinson, 2005).

Etymology.—The new genus-group name is a combination of the Greek words *pharci* (meaning, "a wrinkle"), for the convex ridge in the membrane of the wing that forms the anal brace, and *phyzelos* (meaning, "shy"), in recognition of the rarity of Pottsville Formation insect fossils from Alabama. The name is masculine.

Discussion.—The family Homoiopteridae was established by Handlirsch (1906b) to contain several species of insects from the Upper Carboniferous of Commentry, France, and was later revised by Kukalová (1969), who noted that "...the families Homoiopteridae, Breyeriidae

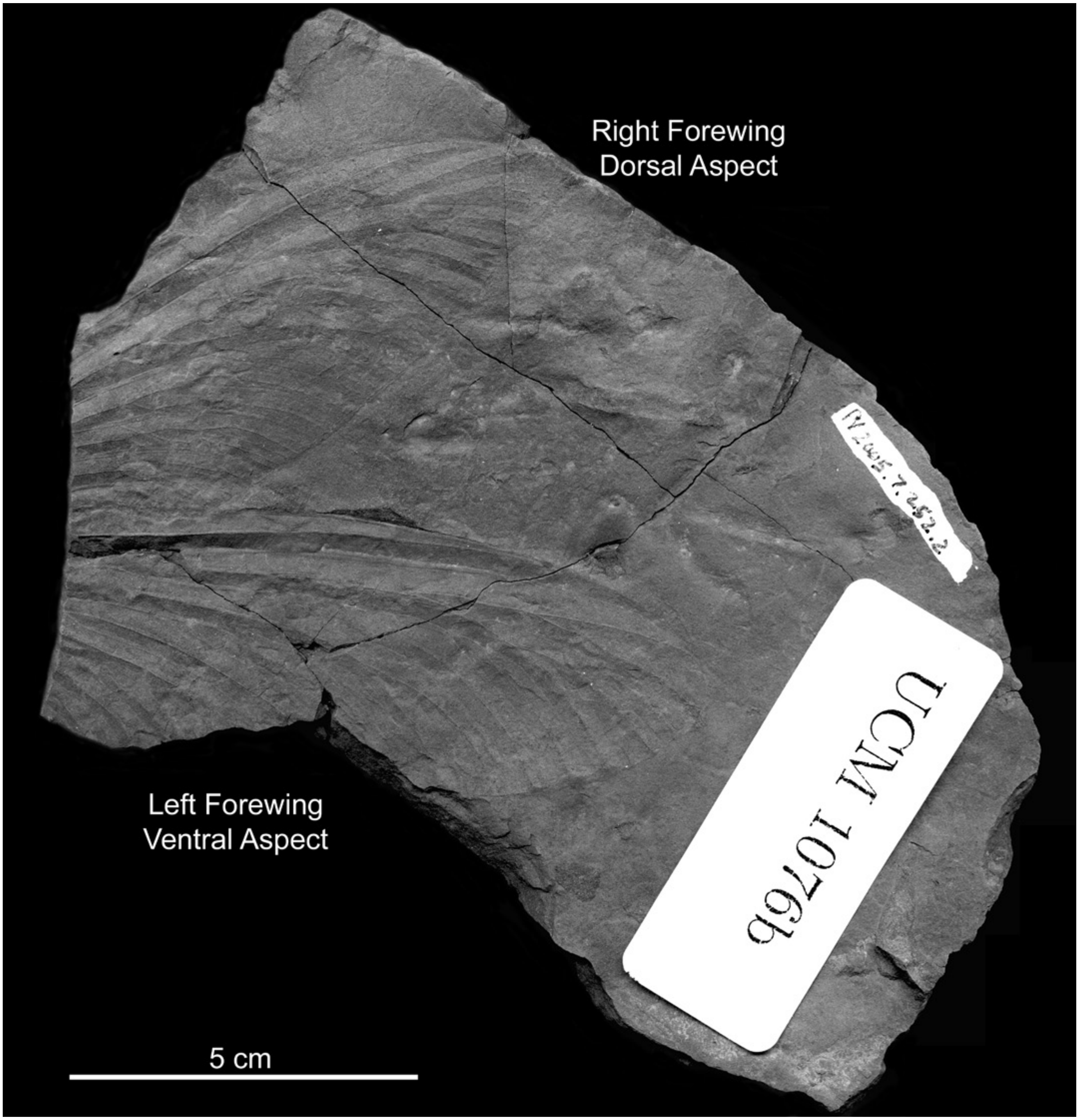

Fig. 4. Photomicrograph of holotype (UCM 1076b, counterpart) of *Anniedarwinia alabamensis* new genus and species (Syntonopterodea: Syntonopteridae) (PV2005.7.2.252.2).

[Handlirsch, 1906b], Graphiptilidae [Handlirsch, 1906b], and Lycocercidae [Handlirsch, 1906a] form a phylogenetic unit...” She also stated that, unlike Breyeriidae and Graphiptilidae, Homoiopteridae and Lycocercidae shared a pronounced bend in the stems of the main veins in the basal third of the wings. She noted that CuA was simple and curved in Lycocercidae, but branched in Homoiopteridae, and that the latter family was also characterized by a “scleroterized strip posterior to the costa.” In addition, Kukalová indicated that she had seen the strip in most of the Homoiopteridae specimens she reviewed, but the strip has seldom been cited in subsequent descriptions of homoiopterid taxa. In 1983, Kukalová-Peck and Richardson described *Mazonopterum wolfforum* and assigned it to Homoiopteridae; the species had CuA simple, but the authors did not comment on having therein compromised one of the distinguishing characters between Lycocercidae and Homoiopteridae. In that same paper they synonymized *Roechlingia hitleri* Guthörl, 1933 [corrected from "*Röchlingia*" to *Roechlingia* by Brauckmann and Becker, 1992] with *Scepasma gigas* Handlirsch, 1911; the holotype of *R. hitleri* had a simple CuA and by implication *Scepasma* would have shared this character; later, Brauckmann and Becker (1992) reinterpreted the fossil of *S. gigas* and verified the simple CuA and described an additional species, *S. mediomatricorum*. Carpenter (1992c) continued to list "CuA simple" as a character of Lycocercidae, "CuA branched" as characteristic of the Homoiopteridae, although he listed *Mazonopterum* as a homoiopterid. He placed *Scepasma* in family *incertae sedis*, based on the holotype's fragmentary nature, apparently missing the additional material represented by *Roechlingia*. Most recently, Prokop et al. (2006) described *Anglopterum magnificum* as a new species of Homoiopteridae; it possessed CuA simple.

Kukalová-Peck and Richardson (1983) listed another character of the new species of Homoiopteridae they described (*Mazonopterum wolfforum*, *Larryia osterbergi*, and *Turneropterum turneri*): an anal brace comprised of a convex ridge in the wing membrane in the form of an arc that tied the bases of the anal veins together. They went back and reviewed other previously described Homoiopteridae [*Boltopruvostia robusta* (Pruvost, 1919), *Homoioptera woodwardi* Brongniart, 1893, *Homoioptera gigantea* Agnus, 1902, *Ostrava nigra* Kukalová, 1960, *Scepasma gigas* Handlirsch, 1911, *Thesoneura americana* Carpenter, 1944], and found that all shared this convex anal brace. Prokop et al. (2006) also found the anal brace to be present on *A. magnificum*. Kukalová-Peck (1997b), in a discussion of basal arthropod structures, identified the "anal brace…formed by [a] stiffened membrane in conjunction with the basal portion of AA" as an autapomorphy of the Palaeoptera. However, the brace has never been described as present on any lycocercid species, and we are unaware of it having been identified in other families of Palaeodictyoptera (although it should to be noted that this structure might easily be interpreted as a taphonomic artifact and missed unless one were specifically looking for it).

Pharciphyzelus lacefieldi new species, possesses both a simple CuA and an anal brace formed by a convex ridge in the wing membrane. We thus place *P. lacefieldi* in the family Homoiopteridae rather than Lycocercidae, noting in passing that the family Lycocercidae should at some point in the future be revisited and reinterpreted to clarify its relationship to and distinction from Homoiopteridae.

Pharciphyzelus new genus differs from most Homoiopteridae genera in having CuA simple. As opposed to *Mazonopterum*, *Pharciphyzelus* new genus has a shorter and more sharply curved stem of MP, the stems of M, CuA, and AA1 are more sharply bent (22°/11°, 36°/24°, 38°/33°, respectively); stem of Cu nearly bisects angle between CuA and CuP in *Pharciphyzelus*, stem of Cu parallel to CuP with CuA arching sharply forward in *Mazonopterum*. *Pharciphyzelus* differs from *Scepasma* and *Mazonopterum* in having more numerous and more closely spaced branches of MP and in CuP sinuous rather than straight to smoothly posteriorly curved. *Anglopterum* has a very wide field between RP and MA and between the stem of M and CuA while these fields are moderately wide in *Pharciphyzelus*.

Pharciphyzelus lacefieldi new species
Fig. 5

Palaeodictyoptera sp.; Lacefield, 1993: 11, unnumbered fig.
Palaeodictyopera sp.; Lacefield, 2000: 68, unnumbered fig.
Breyeria sp.; Atkinson, 2005: 173–174, fig. 4.

Diagnosis.—As for the genus (*vide supra*).

Description.—Basal portion of wing, 76.1 mm long, 38.4 mm wide (estimated to comprise 70% of total wing length, estimated total length ca. 105 mm). Preserved portion of ScP closely paralleling R; maximum distance between costal margin and ScP 5 mm, distance between ScP and R 2 mm; stems of M and Cu parallel and contiguous but not coalesced; stems of R, M, and Cu straight and parallel until Cu diverges sharply posteriorly, at which point R and M are prominently arched and reflexed; between separation of RP from RA and first branching of RP, the costal margin, ScP, RA, RP, and MA nearly straight, parallel and closely spaced; RP distally branched (Fig. 5A); stem of RP longer than stem of R; stem of M from divergence of CuA longer than stem of MP; stem of CuP nearly twice as long as stem of Cu after divergence from M; anterior branch of CuP following a sinuous course initially, diverging from CuA, then converging toward CuA at posterior wing margin; anal veins numerous and densely branched, anal veins branch basally; course of anal, cubital, and medial veins initially smooth, but become reticulate as posterior margin is approached; crossveins fine and densely reticulate; convex ridge in the form of an arc through membrane in anal area forming an anal brace that passes through the anal veins at a nearly perpendicular angle, located at a radius of about 1 cm from preserved base.

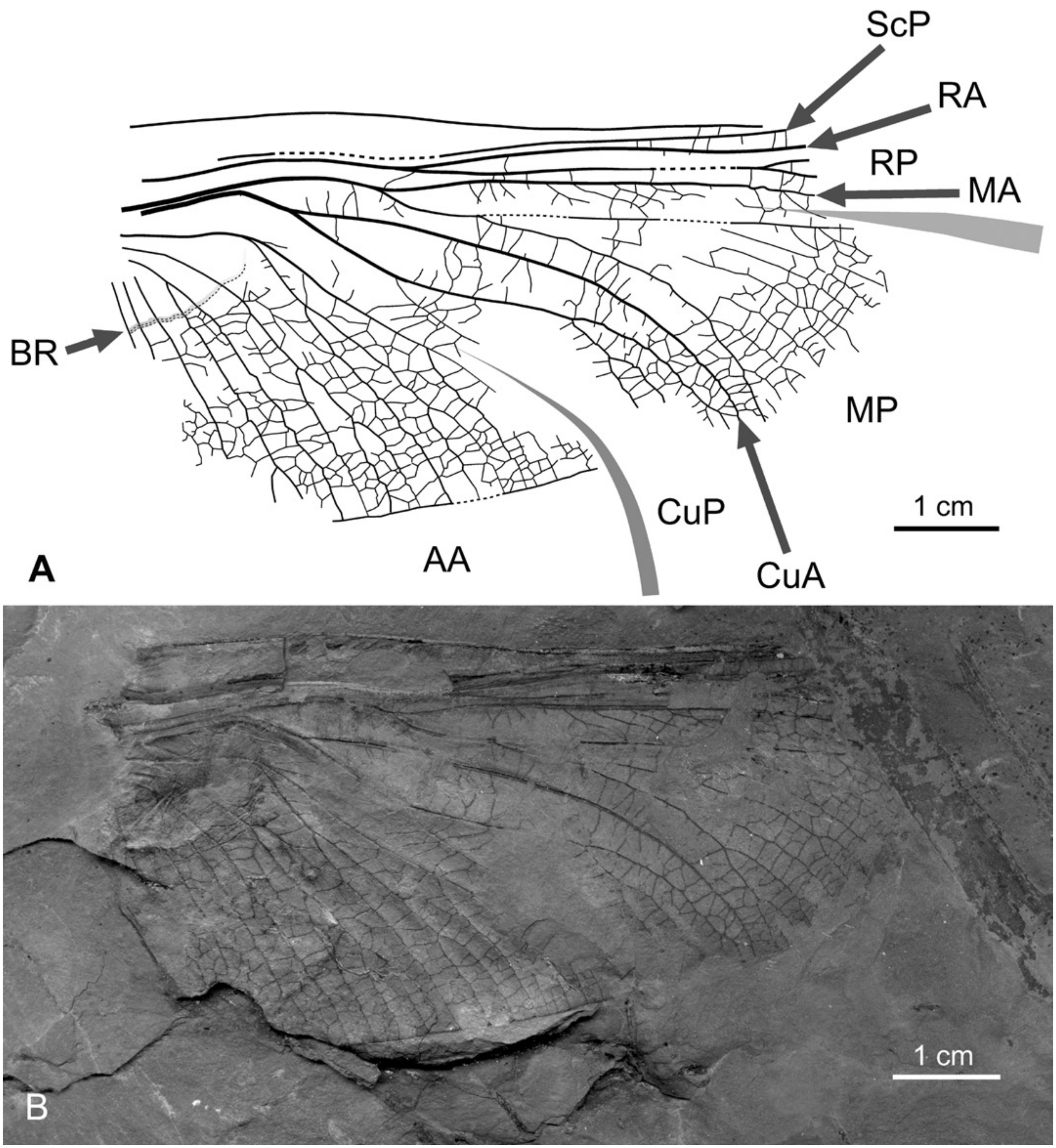

Fig. 5. *Pharciphyzelus lacefieldi* new genus and species (Palaeodictyoptera: Homoiopteridae): A. Reconstruction of wing venation; BR denotes anal bridge formed by convex ridge of stiffened membrane *sensu* Kukalová-Peck and Richardson (1993). B. Photomicrograph of holotype (no known counterpart), comprising basal 70% of forewing (PI1993.0001.0001).

Holotype.—PI993.0001.0001 (Fig. 5B), University of Alabama Museum of Natural History, Tuscaloosa, Alabama; partial forewing in dorsal aspect; no counterpart; Pottsville Formation (Pennsylvanian), coal mine 2 mi N. of Eldridge, Walker County, Alabama, 16 January 1993, J. Lacefield collector.

Etymology.—The specific epithet is a patronym honoring Jim Lacefield, Alabama geologist and paleontologist and collector of the holotype.

Order DIAPHANOPTERODEA Handlirsch, 1919
Family NAMURODIAPHIDAE
Kukalová-Peck & Brauckmann, 1990

Camptodiapha new genus

Type species.—*Camptodiapha atkinsoni* Beckemeyer and Engel new species.

Diagnosis.—Stems of ScP and R straight at wing base, without deflection (Fig. 6A); MA with sharp bend at convergence with RP, veins do not coalesce but are joined by short crossvein; CuA with sharp bend at convergence with M but veins do not coalesce (presence or absence of crossvein unknown because of defect in rock surface: Figs. 6A, 7); ScP terminating on costal margin distal to wing midlength but well short of apex; MA and CuA unbranched (Fig. 6A); RA and anterior branch of RP parallel and widely separated over distal half of wing; RP with six branches; MP with seven branches; CuP with at least three branches preserved; all branching of longitudinal veins dichotomous. Differentiated from Diaphanopteridae: *Diaphanoptera* by MA and RP and CuA and M converging but not coalescing and with short crossveins versus coalescence in Diaphanopteridae, and by CuA and CuP well separated and not convergent with a short crossvein as in *Diaphanoptera* (Béthoux and Nel, 2003).

Etymology.—The new genus-group name is a combination of the Greek word *kamptos* (meaning, "bending" or "flexible"), in reference to the sharply bent longitudinal veins MA and CuA, and the suffix *diapha*, from the family name. The name is feminine.

Discussion.—The family Namurodiaphidae is rare and heretofore known only from a single specimen, *Namurodiapha sippelorum* Kukalová-Peck and Brauckmann, 1990. The holotype is a nearly complete insect from Hagen-Vorhalle of Germany and was deemed to be of particular interest since it possessed what was presumed to be a primitive form of wing bracing through coalescence of MA and RP and of CuA and M, a feature that is present in certain palaeopterous insects and some Neoptera. In this family, coalescence does not occur, but the veins converge and are connected by a short crossvein. The occurrence of *Camptodiapha atkinsoni* in the Pennsylvanian Pottsville Formation extends the range of the family to North America. The new species is roughly twice the size of *N. sippelorum*, which had a wing length of 37 mm.

Sinitshenkova (2002) and Grimaldi and Engel (2005) both placed the family Namurodiaphidae in Megasecoptera, although Kukalová-Peck and Brauckmann described it in Diaphonopterodea. However, the trimerous tarsi, absence of an archedictyon, and simple MA support, as does the putative presence of neopterous wing flexion, inclusion of the family within Diaphanopterodea and we accordingly return the family to this order.

Camptodiapha atkinsoni new species
Figs. 6–7

Diagnosis.—As for the genus (*vide supra*).

Description.—Hind wing (determined by straight anterior margin of wing), 71.7 mm preserved length, 74 mm estimated total length, maximum preserved width 19.3 mm, estimated maximum width 21 mm; basal third of wing missing anterior to R; measurements in mm distal to origin CuA: stem of M diverging from R at 5.8 mm; CuA diverging from M (closest convergence of CuA and M) at 5.6 mm; first branch CuP at 8.5 mm; origin MA 10.7 mm; origin RP at 12.9 mm; MP forking 8.9 mm distal to origin MA; MA bending sharply at point of closest convergence with RP at 8.9 mm, short crossvein joining MA and RP; ScP intersecting costal margin at two-thirds wing length; first branch of RP 24.7 mm distal to origin RP, RP with six branches; in distal half of wing RA and anterior branch RP roughly parallel and separated by 2 mm; branches of RP intersecting posterior wing margin in distal quarter of wing; MA unbranched, terminating beyond three-quarters wing length; MP forking at level of MA convergence with RP, MP with seven branches, all terminating on posterior margin beyond wing midlength, intersecting margin at angles of 60 ± 5^{o}; CuA unbranched, bending sharply at convergence with M, although only short stem of MA after origin preserved (Fig. 7); missing portion of CuA between origin and convergence with M (so it is unknown whether or not there were m-cua crossveins: Fig. 7); CuA termination not preserved (posterior third of basal half of wing distal to AA2 missing); CuP with at least three branches, but portions of branches distal to forking missing; preserved portions of anal veins branched; crossveins faint and poorly preserved, but straight and not reticulate. Counterpart comprising distal two-thirds of wing less anterior margin, distal half showing only course of longitudinal veins through an obscuring thin layer of matrix; portion of wing membrane (where revealed) with an irregular banded color pattern.

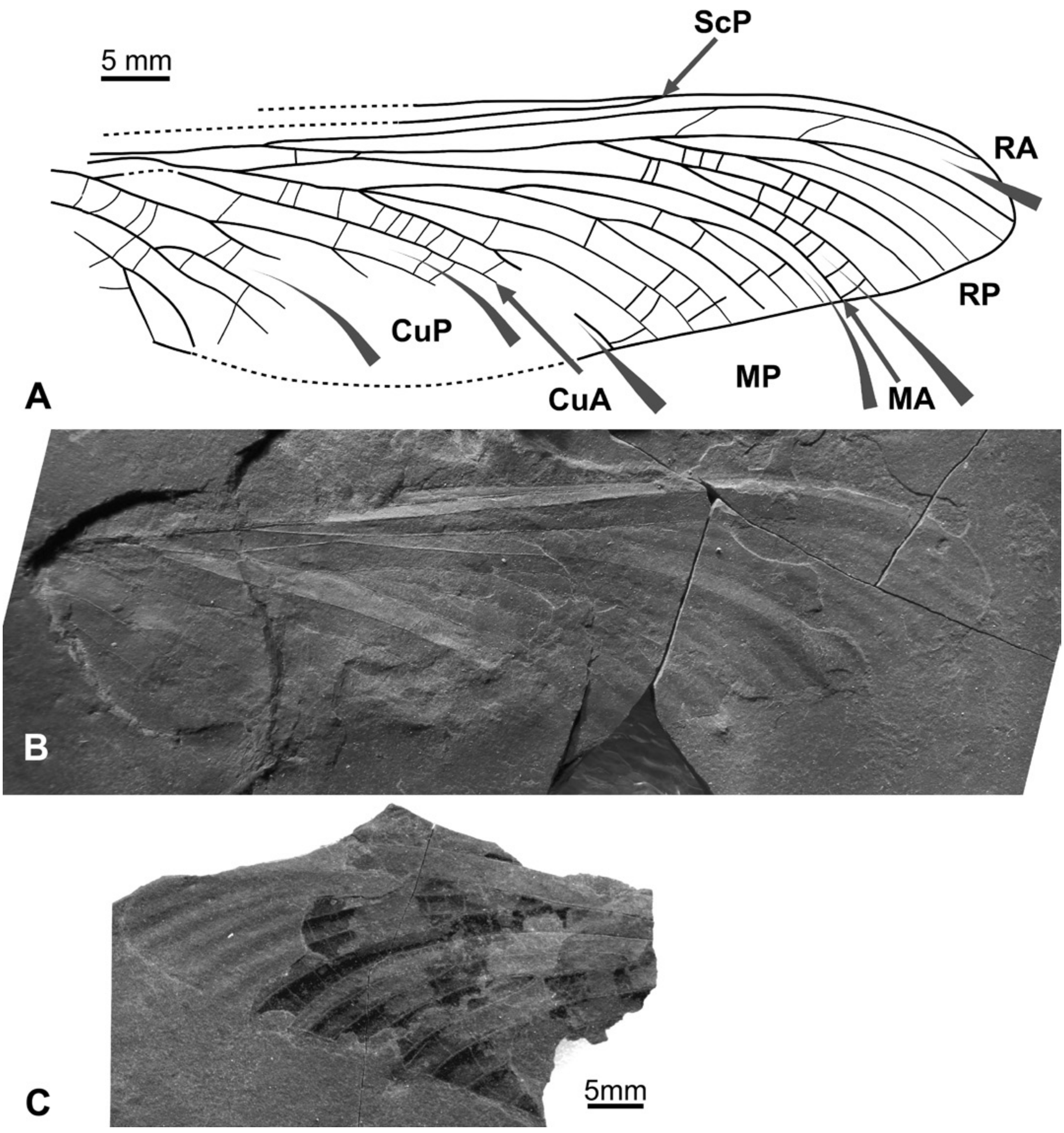

Fig. 6. Hind wing of *Camptodiapha atkinsoni* new genus and species (Diaphanopterodea: Namurodiaphidae): A. Reconstruction of wing venation. B. Photomicrograph of part (WSC#MSC9334 – UCM3045) comprising nearly complete wing in dorsal aspect absent only the very base; to same scale as in figure 6A. C. Photomicrograph of counterpart, posterio-distal half of wing in ventral aspect, portion of membrane covered by thin layer of matrix, visible portion of wing membrane revealing extensive color pattern.

Holotype.—WSC#MSC9334 (UCM3045), McWane Science Center; part a nearly complete hind wing lacking posterior portion of basal half and costal region anterior to R in basal third (Fig. 6B), counterpart representing

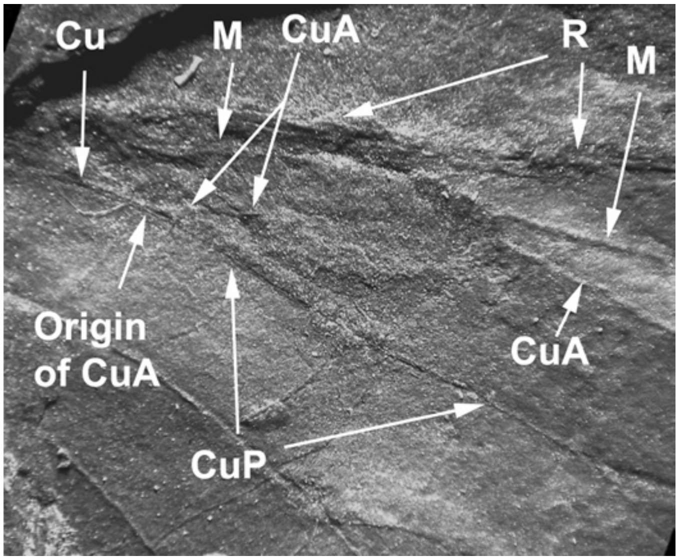

Fig. 7. Details of base of radial-cubital space and portions of CuA in hind wing of *Camptodiapha atkinsoni* new genus and species (Diaphanopterodea: Namurodiaphidae). The preserved portion of the branch of CuA at its origin, and the preserved course of CuA after its convergence with M allow reconstruction of the course of CuA as illustrated in figure 6A. The missing portion of the rock surface likely contained a crossvein between CuA and M similar to the one between MA and RP (Fig. 6).

the distal 60% of wing lacking anterior margin and with a thin layer of matrix covering the details of wing venation and membrane over all but the central third of the wing (Fig. 6C); specimens on thin slab of rock roughly 2 mm thick that was found in association with tetrapod trackways; Pottsville Formation (Pennsylvanian), Union Chapel Mine, Walker County, Alabama; March 2005, P. Atkinson collector.

Etymology.—The specific epithet is a patronym recognizing Dr. T. Prescott Atkinson, collector of this and several other insect specimens from the Union Chapel Mine locality; he is one of the Alabama Paleontological Society members responsible for the protection and preservation of this important fossil locality.

Order MEGASECOPTERA Handlirsch, 1906a
Suborder EUBLEPTOPTERA Crampton, 1930
(=Eubleptidodea Laurentiaux, 1953)
Family ANCOPTERIDAE Kukalová-Peck, 1975

Ancopteridae Kukalová-Peck, 1975: 3. Type genus: *Ancoptera* Kukalová-Peck, 1975.

Diagnosis.—Wings slender, but apparently not petiolate; almost equally broad to slightly tapered beyond wing midlength; apex broadly rounded to slightly tapered; ScP extending beyond wing midlength; ScP and RA close to costal margin distally; bases of R and M not coalesced but stem of RP and M may be contiguous near base; RP arising basally; M branching proximally; MA and CuA simple; RP, MP, and CuP branched; costal margin nearly straight but briefly convex basal to or at wing midlength; crossveins numerous, forming intercalary veins; posterior margin of wing sinuous to mildly undulate.

Comments.—The family Ancopteridae was established by Kukalová-Peck (1975) for the Lower Permian genus, *Ancoptera* Kukalová-Peck, 1975, from the Moravian Obora deposits. *Ancoptera* is much broader, less slender, and has a straighter and less concave costal margin and a much more undulatory posterior margin than *Agaeoleptoptera*. The major venational characteristics listed in the familial diagnosis are consistent with those identified for Ancopteridae by Kukalová-Peck (1975) and Carpenter (1992c). The differences (especially lack of definitive preservation of the posterio-basal portion of the wing, the attenuated form of *Agaeoleptoptera* and the almost sinuous rather than undulatory posterior margin) might be sufficient to warrant establishment of a new family. However, we prefer to take a conservative approach and place the new genus within Ancopteridae, extending the definition and expanding the geographic range and temporal extent of the family. If additional material is found in the future, this assessment may have to be revisited.

KEY TO GENERA OF ANCOPTERIDAE

1. Wing long but only slightly narrow, with broadly rounded apex (wing length about 4–5 times width), wing nearly same width distad and basad midwing; posterior margin with mild undulations; costal margin straight with slight convexity in basal third; RP branches in basal third of wing (Lower Permian: Obora, Moravia, Czech Republic)....................*Ancoptera* Kukalová-Peck

—. Wing very long and narrow with slightly tapered apex (wing length about 7 times width), wing tapered and narrowed slightly distad midwing; posterior margin slightly sinuous; costal margin nearly straight with definite convexity at midwing; RP branches nearer midwing (Upper Carboniferous: Union Chapel Mine, Alabama, USA)................... *Agaeoleptoptera* new genus

Agaeoleptoptera new genus

Type species.—*Agaeoleptoptera uniotempla* Beckemeyer and Engel new species.

Diagnosis.—Wing extremely slender, apparently not petiolate, slightly narrower distally than basal to midwing, posterior margin slightly sinuous (Fig. 8A); costal margin, ScP, and RA all parallel and very close together distally; RP apparently separating from RA at extreme base of wing, RP with three terminal branches; RP and M contiguous proximally (Fig. 8A); stem of M very short; MA and CuA simple (Fig. 8A); MP and CuP branched; intercalary veins in radial and medial fields.

Etymology.—The genus-group name is a combination of the Greek words *agaios* (meaning, "elegant"), *leptos* (meaning, "slender"), and *pteron* (meaning, "wing"). The name is feminine.

Agaeoleptoptera uniotempla new species
Fig. 8

Megasecoptera sp.; Atkinson, 2005: 175, fig. 6.

Diagnosis.—As for the genus (*vide supra*).

Description.—Preserved length 80 mm, estimated total length 83 mm; preserved width 11.8 mm; ratio of length to width 7.0, placing it in association with most slender of fossil wings (Kukalová-Peck, 1975); maximum wing width just distal to one-quarter wing length, costal margin with noticeable convexity just basal to wing midlength; posterio-basal portion of wing absent, but impressions of shape visible on matrix of part indicate base of wing to be broad rather than petiolate (Fig. 8.1); only basal and terminal portions of ScP preserved, ScP terminating at three-quarters wing length; costal margin, ScP, RA, and RP each separated by about 1 mm at 10% of wing length; RA nearly straight, with slight curvature, terminating near apex; RA-RP branching not preserved, RP contiguous with M in basal 10% of wing (Fig. 8A); portion of RP from 40% wing length to about 70% wing length not preserved, branching of RP not preserved, but with three terminal branches, with numerous intercalary veins, RP field in terminal 15% of wing length; MA simple, branching from M at 15% wing length, terminating at 83% wing length; first MP fork just basal to wing midlength, MP with three terminal branches and several intercalary veins (Fig. 8A); CuA and MP parallel and well separated (about 1 mm) basally, CuA and anterior branch of CuP not preserved beyond wing midlength, estimated that CuA would terminate at 60% wing length; CuP and AA1 not preserved in basal 20% of wing; AA1 terminating at about 40% wing length; few crossveins preserved.

Holotype.—PV2005.0007.0260.001 (UCM2368) (part) (Fig. 8B) / PV2005.0007.0260.002 (UCM2369) (counterpart) (Fig. 8C), University of Alabama Natural History Museum, Tuscaloosa, Alabama; nearly complete wing on large slabs (approximately 30 by 40 cm) that also contain fossil plant material; Pottsville Formation (Pennsylvanian), Union Chapel Mine, Walker County, Alabama, P. Atkinson collector.

Etymology.—The specific epithet is a combination of the Latin terms *unio* (meaning, "union") and *templum* (meaning, "temple"), in recognition of Union Chapel, the namesake of the mine that is the type locality for the species.

SUPERORDER ODONATOPTERA LAMEERE, 1900

Order PROTODONATA Brongniart, 1893
Family PARALOGIDAE Handlirsch, 1906b

Genus *Oligotypus* Carpenter, 1931
Oligotypus tuscaloosae new species
Fig. 9

Diagnosis.—Large and slender species (130–160 mm in total length) with costal margin concavely curved, ScP terminating on costal margin near midwing, posterior branches of longitudinal veins terminating more nearly perpendicular to posterior wing margin (Fig. 9), terminations of longitudinal veins more basal than in other *Oligotypus* species.

Description.—Distal half of forewing (basal half of forewing, hind wing, body unknown): preserved length 77 mm, estimated to comprise distal 50–60% of wing length, estimated length of complete wing 130–160 mm; wing slender, maximum width 23 mm; ScP intercepting costal margin 46 mm basal of wing apex, estimated to be roughly three-quarters of wing length from base; distance between costal margin and ScP equal to distance between ScP and RA at level of initial branching of RP; RA very closely paralleling costal margin distal to termination of ScP (Fig. 9A); anterior branch of RP diverging from RA distal to termination of ScP; branches of RP widely divergent; MA unbranched, parallel to posterior branch of RP; anterior branch of MP parallel to MA, MA branching slightly distal to RP branching; MP roughly parallel to posterior branch of MA; crossveins not well preserved.

Holotype.—PI1988.001.001 (Fig. 9B); Alabama Museum of Natural History, University of Alabama, Tuscaloosa, Alabama; single wing (no counterpart) representing forewing (on basis of maximum convexity of posterior margin near wing midlength) in ventral aspect, extending from just distal of branching of RP to near apex of wing; Pottsville Formation (Pennsylvanian), "In spoil pile", strip mine at Wyndam [sic: correct spelling Windham] Sprs., Tuscaloosa County, Alabama, 1 October 1988, J. Hall, K. Gaddy, collectors.

Etymology.—The specific epithet recognizes the legendary Mississippian Chief Tuscaloosa, famous for leading a battle against the conquistador Hernando de Soto

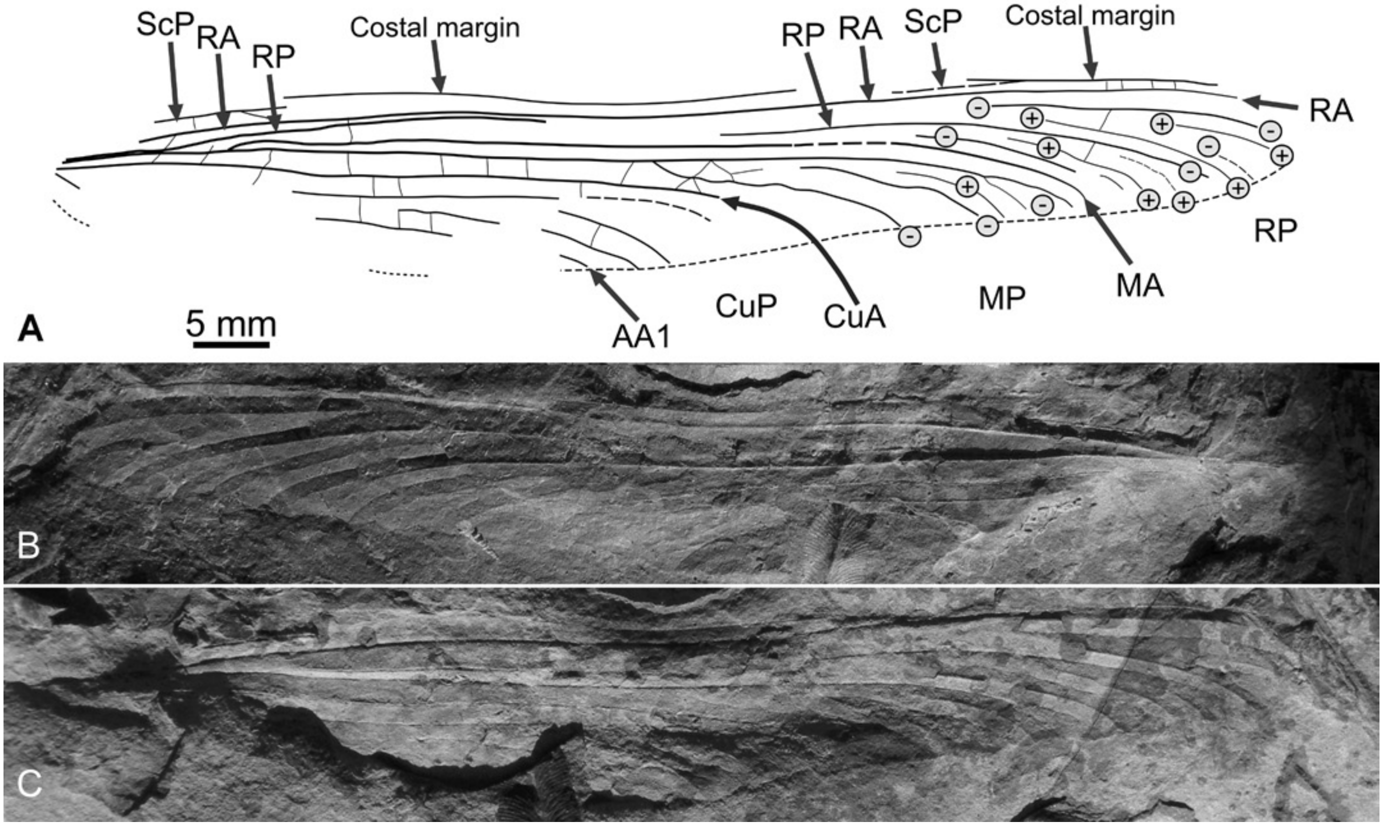

Fig. 8. *Agaeoleptoptera uniotempla* new genus and species (Megasecoptera: Ancopteridae): A. Reconstruction of wing venation with convexity (+) or concavity (-) of wing in dorsal aspect noted. B. Photomicrograph of part (UCM2368) (PV2005.007.0260.001). C. Photomicrograph of counterpart (UCM2369) (PV2005.007.0260.002). Photographs and illustration to same scale.

and for whom the city and county of Tuscaloosa, Alabama were named.

Discussion.—Paralogidae occur over a wide area of the central and eastern United States in North America, with specimens recorded from the Permian of Kansas, and the Carboniferous of Rhode Island, Illinois, and now Alabama. Recently, Nel et al. (2009) reported the first paralogid from Europe, describing the new species *Paralogopsis hispanicus*, from Cordoba, Spain. The family Paralogidae was established by Handlirsch (1906b) for the genus *Paralogus* Scudder, 1893, to which he added his genus *Paralogopsis* Handlirsch, 1911, a few years later. Carpenter (1931) subsequently described the genus *Oligotypus*, and many years later newly circumscribed the family, relegating *Paralogopsis longipes* Handlirsch, 1911 to family *Incertae sedis* (Carpenter, 1960, 1992c). Carpenter (1960) also provided corrections to portions of Scudder's (1893) description and Fraser's (1957) illustration and discussion of *Paralogus*. Carpenter (1960) noted that the major differences between the two paralogid genera are the much greater convexity of the posterior margin of the wing in *Paralogus*, and the true branching of the veins in the MA field of *Paralogus* as opposed to the irregular venation pattern of the origins of the veins in the MA field in *Oligotypus*. Nonetheless, all paralogids have ScP terminating nearer the wing midlength than the apex, the branches of RP widely divergent, and a relatively reduced number of crossveins by comparison with Meganeuridae.

Oligotypus tuscaloosae differs from *O. tillyardi* Carpenter, 1931 in overall size (the wing of the latter species is 50 mm long and 11 mm wide, about a third the size of the new species), and in being more slender (width to length 5.6–7 mm in *O. tuscaloosae*, 4.5 mm in *O. tillyardi*). The longitudinal veins and branches terminate at a more nearly perpendicular angle to the posterior wing margin in *O. tuscaloosae* and in *Paralogus* versus at more nearly acute angles in *O. tillyardi* and *O. makowski* Carpenter and Richardson, 1971; thus the terminations of the longitudinal veins in *O. tuscaloosae* are more basal than in *O. tillyardi* and *O. makowski*. It should be noted that Nel et al. (2009) recently revised the Permo-Carboniferous griffenflies, and questioned the placement of *O. makowski* in Paralogidae; they did not, however, definitively assign the species to another family. We therefore compare *O.*

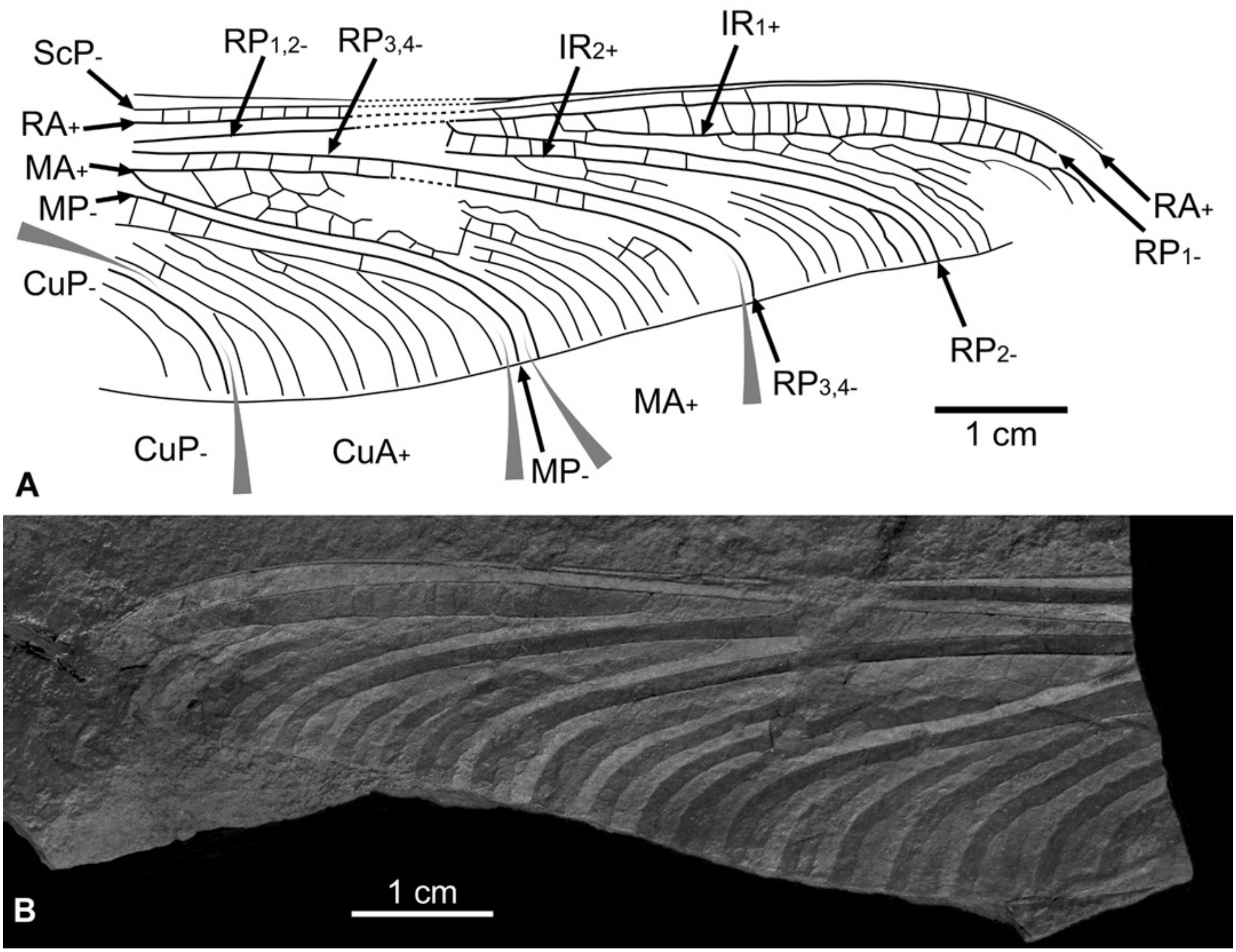

Fig. 9. *Oligotypus tuscaloosae* new species (Protodonata: Paralogidae): A. Reconstruction of wing venation, with venational nomenclature following that of Riek and Kukalová-Peck (1984) as amended by Nel et al. (1993), Bechly (1996), Fleck et al. (2003), and Rehn (2003); the use of "+" or "–" after a vein identity indicates convexity or concavity, respectively. B. Photomicrograph of holotype; distal half of forewing in dorsal aspect (PI1988.0001.0001).

tuscaloosae with both *O. tillyardi* and *O. makowski*. Carpenter and Richardson (1971) estimated *O. makowski* to be 90 mm in length and 18 mm wide for a ratio of 5.0, nearly as slender as *O. tuscaloosae*, and both species have a more tapered apex than that of *O. tillyardi*. The forewing ScP terminates more distally in *O. tuscaloosae* than in the other *Oligotypus* species. That and the sharp bend of the longitudinal veins toward the posterior margin means that ScP terminates at the level of termination of MP in *O. tuscaloosae*, but at the level of termination of CuP in the other species of *Oligotypus*. The argument might be made that the sum of these differences would be sufficient for us to have established a new genus for *O. tuscaloosae*. However, since the description is based solely on the distal half of the wing, we prefer to take the more conservative stance of placing the species as basal within *Oligotypus* for the moment and until more completely-preserved material is discovered.

DISCUSSION

To date the insects recovered from the Pottsville Formation are all of palaeopterous orders, lineages that were diverse and abundant during the Late Paleozoic. While indicative of a unique fauna, all of the taxa recovered thus far exhibit connections with other major deposits in North America and Europe. Given the diversity of primitive neopteran insects, including early Dictyoptera, present in other Carboniferous deposits in North America, it is surprising that such taxa have not been recovered yet from the deposit in Alabama. Although insects are not abundant in the deposit, continued excavation likely will reveal additional diversity, particularly primitive Neoptera, and perhaps including Paoliidae, putatively the most basal lineage of neopteran insects. The Pottsville insects are of considerable interest given that they are the southeasternmost records of Upper Carboniferous insects in the United States and thereby represent an interesting biogeographic comparison with the well documented and more northerly or western faunas of Illinois, Pennsylvania, and Kansas. The current sampling, while small, highlights that numerous lineages were present and that insects should be intensely sought from the Pottsville Formation. In addition, all of the specimens recovered to date are of larger insects and it is possible that past collecting efforts overlooked more faintly preserved or minute wings, representing the vast majority of insect diversity (Carpenter, 1992c; Beckemeyer and Hall, 2007), even during the hyperoxic atmospheres of the Late Paleozoic. Thus, the potential value of material from these deposits is considerable for their broader implication to understand Late Paleozoic insect diversity and distributions.

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