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Discovery of an enigmatic and gigantic Pennsylvanian Archaeorthoptera

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Abstract

The species *kiarae sp. nov.* is described on the basis of an incomplete fossil specimen yielded by the Pennsylvanian deposit of Piesberg near Osnabrück (Germany). A second incomplete specimen is tentatively assigned to the species. The species is erected under the new cladotypic nomenclatural procedure, but a proper Linnaean name is also provided (*Forfexala kiarae gen.* and *sp. nov.*). The holotype (and most complete specimen) is interpreted as a hind wing, and the species assigned to the taxon *Archaeorthoptera*. The combination of a simple CuPa, a common stem MP + CuA (diverging from M + CuA) separating into MP and CuA at the point of fusion of CuA with CuPa, a brief connection of the anterior branch of MA with RP, and a branched CuPb, indicate that the new species does not belong to any of the *Archaeorthoptera* groups previously reported in the Pennsylvanian. According to the estimated hind-wing length of the species (ranging from 85 to 100 mm), *kiarae sp. nov.* is the largest *Archaeorthoptera* of the period, and one of the largest ever. The new species shares the habitus of phasmatodeans, but definitive assignment to this group would require new investigations of the wing venation of its representatives.

Key words

fossil insect, hind wing venation, Upper Carboniferous, *Archaeorthoptera*, *kiarae*, *Forfexala*, Phasmatodea, cladotypic nomenclatural procedure

Introduction

A number of recent revisions allowed Carpenter's (1992) protorthopteran wastebasket to be disassembled, and provided a clearer view of Pennsylvanian relatives of orthopterans. Together with their extant relatives, these fossil species are included in the taxon *Archaeorthoptera* Béthoux & Nel, 2002, *dis.-typ.* Béthoux, 2007d. Besides the more derived caloneurodeans, gerarids, and genuine stem orthopterans known during the Pennsylvanian, two main groups have been identified so far, namely the cnemidolestodeans (see Béthoux 2005a) and the lobeattids [see Béthoux (2005b), Béthoux (2008a), and Prokop & Ren (2007)]. The latter groups have been reported from various deposits, and several species are known after several specimens. Apart from these groups, a few species such as *dumasii* Brongniart, 1879 and *spilopterus* Handlirsch, 1911 [see Béthoux (2003) and Béthoux (2006), respectively; see also Béthoux & Nel (2004, 2005)], known after a limited number of specimens, might occupy a more basal position within *Archaeorthoptera*. Since the position of phasmatodeans among hexapodans is being debated at the moment [compare Gorokhov & Rasnitsyn (2002) and Beutel & Gorb (2006) on one hand, and Terry & Withing (2005) and Kjer *et al.* (2006) on the other], its subordination within *Archaeorthoptera* must be considered as a working hypothesis only.

Hereafter we erect a new species belonging to *Archaeorthoptera* on the basis of an incomplete Pennsylvanian wing. Another fragmentary specimen that might belong to the same species is described. This species exhibits a combination of character states that challenges its assignment to any of the archaeorthopteran groups previously identified.

As readers could have noted already, a nomenclatural procedure, alternative to the traditional Linnaean one, is used in this contribution, namely the cladotypic nomenclatural procedure elaborated by Béthoux (2007b, c). Under this approach, names of species that experienced a cladogenesis event (*i.e.*, taxa) are permanently associated with a definition. A definition aims mainly at substantiating a homology assumption and takes the form: "species that evolved from the metapopulation lineage in which the character state [X], as exhibited by [cladotypic species 1] and [cladotypic species 2], has been acquired". Two specimens belonging to each of the cladotypic species constitute type material ('cladotypes'). The main advantage of this approach is that taxon composition is not subjectively determined (see below) as under the traditional procedure. In addition, a number of falsifiable assumptions besides the 'homology assumption' are related to definitions (Béthoux 2007b, c; Béthoux in press.). If an assumption is not fulfilled, the status of a name as that of a valid taxon can be questioned. For example, if the homology assumption is not fulfilled (*i.e.*, cladotypes acquired the same character state by convergence), a name refers to a polyphyletic assemblage. If the polarity assumption is not fulfilled (*i.e.*, the defining character state is a plesiomorphy), a name refers to a paraphyletic assemblage. The recourse to falsifiable assumptions allows nomenclature to be directly connected to hypotheses.

Regarding names of species that experienced no cladogenesis event, suggestions by Dayrat *et al.* (2004; and references therein) are followed. Species are referred to by a uninomen. Ambiguity due to homonymy is avoided by coupling the uninominal name with authorship information, and/or with a taxonomic address composed of taxa to which the species can be assigned [see Béthoux (2007d, 2008a) and Dayrat (2005) for formal applications; see also Dayrat *et al.* (2005), Angielczyk (2007)]. This 'coupling' is necessary, at least at the first mention of a species (see below). A formal (but implicit) definition is "individuals belonging to the same evolving metapopulation lineage as [holotype specimen]" (Béthoux 2007b). In other words holotypes are maintained. With these premises, recourse to ranks is unnecessary. As a consequence, erection of monotypic genus names is unnecessary (see this contribution). The phylogenetic position of a species can be retrieved immediately from its taxonomic address (Béthoux 2007d).

Besides the description of new fossil material, this paper aims

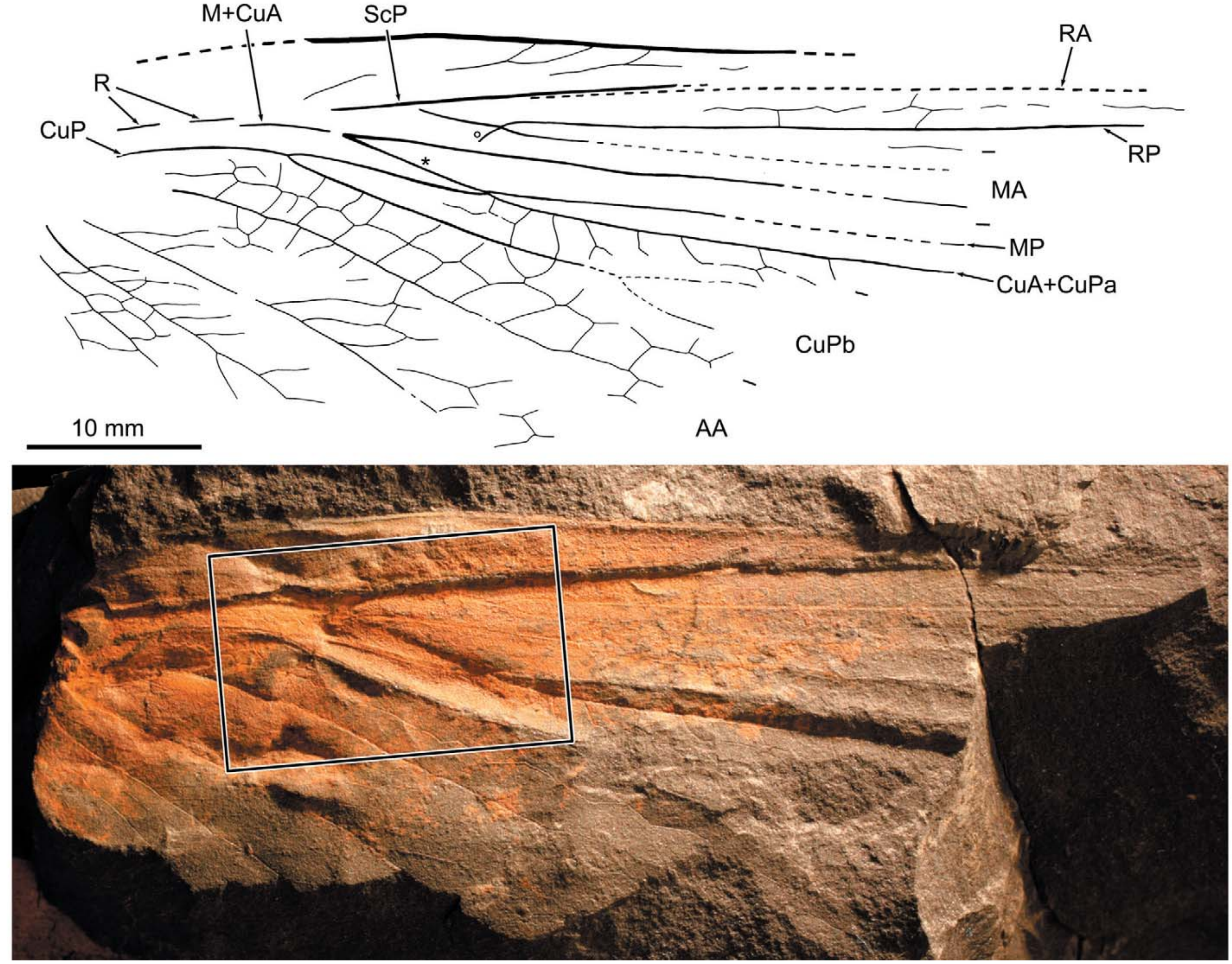

Fig. 1. *Archaeorthoptera kiarae sp. nov.* (holotype specimen IGP In 190, negative imprint); drawing and photograph (negative imprint, reversed); see text for abbreviations; * indicates MP + CuA; ° indicates the anterior branch of MA connecting with RP.

at presenting a routine application of the cladotypic nomenclatural procedure. Comparative merits of the latter will be investigated in more detail elsewhere (Béthoux in press.).

Materials and Methods

Throughout this contribution, traditional taxon names are avoided, and 'vernacularized' names preferred (for example, orthopterans rather than Orthoptera; in addition, all taxon names are written in italics under cladotypic nomenclature). The choice of the nomenclatural procedure is based on the decision of one of us (OB) and does not imply the consent of the second author to all aspects of this procedure. Discussion on the relevance of the cladotypic procedure (see above) is also based on the opinion of the former author only. An appendix compliant with the ICZN is provided, so as to allow mention of the new species under a traditional framework, and to make the new species valid under the ICZN.

The venation patterns and vein widths of the specimens were drawn with a SteREO Discovery V8 stereomicroscope equipped with a pair of W-PL 10x/23 eyepieces, a Plan Apo S 1.0x FWD objective, and a camera lucida. Specimens were observed dry and under ethanol.

The specimens IGP In 190 and IGP In 191 were photographed with cameras Canon EOS 400D and Canon EOS 450D respectively, both equipped with a 50-mm Canon macro lens (1:2.5) and an elongation tube (brand Kenko). Photographs reproduced in Figs 2 and 3 were taken using the light-mirror technique (Béthoux *et al.* 2004). The photograph of Fig. 3 is a composite of a pair of photographs, one taken under dry conditions and one under ethanol.

We use the wing venation nomenclature elaborated by Béthoux & Nel (2002) for *Archaeorthoptera*, itself based on that of orthopterans (Béthoux & Nel 2001), and on the serial insect wing venation pattern (Lameere 1922, 1923). Corresponding abbreviations are repeated herein for convenience: ScP, posterior Subcosta; R, Radius; RA, anterior Radius; RP, posterior Radius; M, Media; MA, anterior Media; MP, posterior Media; CuA, anterior Cubitus; CuP, posterior Cubitus; CuPa, anterior branch of CuP; CuPb, posterior branch of CuP; AA, anterior Analis; AA1, first anterior Analis. A vein (or vein sector) is said to be convex if located on an elevation, and concave if located in a depression. Criticisms expressed by Gorokhov (2005) regarding the homology hypothesis followed herein are addressed in Béthoux (2007a). Subsequent comments by Rasnitsyn (2007) are addressed in Béthoux (2008b).

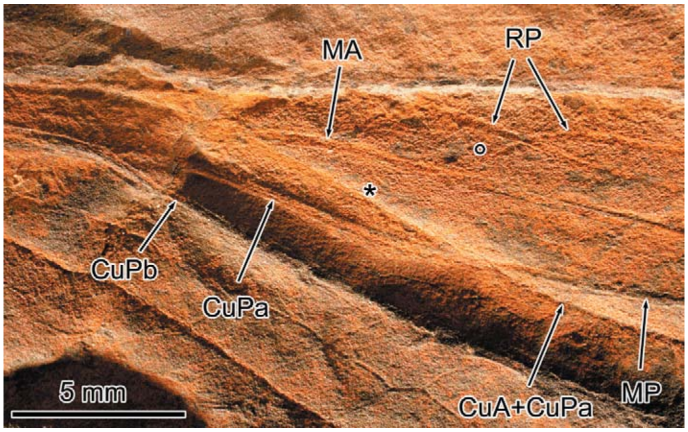

Fig. 2. *Archaeorthoptera kiarae sp. nov.* (holotype specimen IGP In 190, negative imprint); detail of the wing base as located on Fig. 1 (negative imprint, reversed, light-mirrored); * indicates MP + CuA; ° indicates the anterior branch of MA connecting with RP.

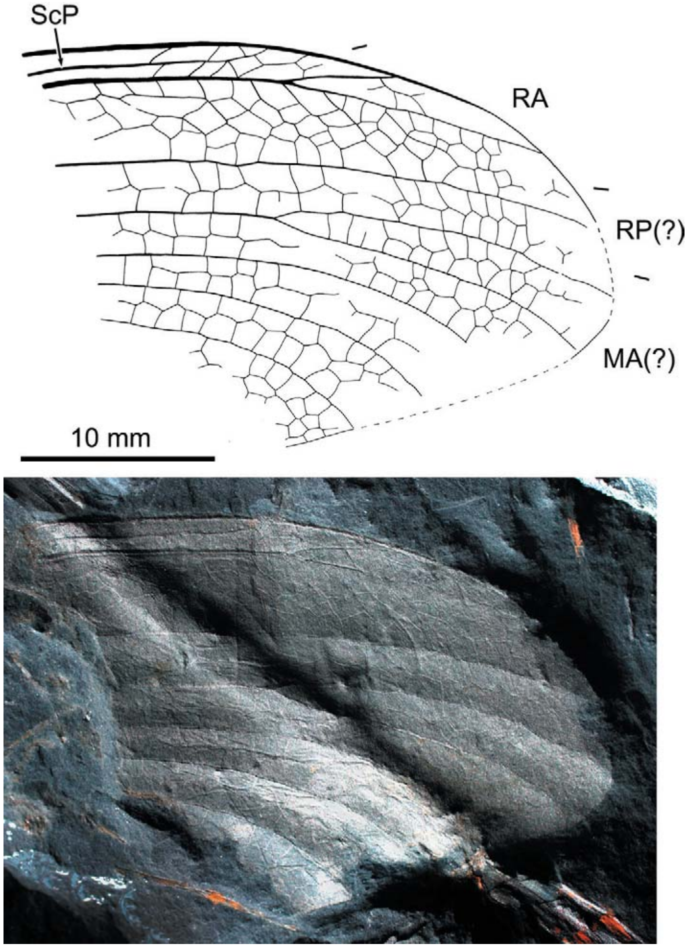

Fig. 3. *Archaeorthoptera kiarae sp. nov.* (specimen IGP In 191, negative imprint); drawing and photograph (negative imprint, reversed, composite, light-mirrored; polarized light).

Systematic Paleontology

Taxon *Archaeorthoptera nom.* Béthoux & Nel, 2002, *dis.-typ.*
Béthoux, 2007d
Species *kiarae sp. nov.*
Figs 1-3

Etymology.—After 'Kiara', name of the granddaughter of the discoverer of the material (Michael Sowiak) (genitive feminine).

Diagnosis.—Hind wing: length of at least 85 mm; RP simple for a long distance; anterior branch of MA briefly connected to RP; M + CuA separated into MA and MP + CuA; MP diverges from MP + CuA at the point of connection with CuPa; CuPb branched; cross-venation network loose with intercalary secondary veins.

Material.—Specimen IGP In 190 (holotype), negative imprint, and specimen IGP In 191 (wing fragment; tentatively assigned to *kiarae sp. nov.*, see below), negative imprint, both housed at the Institute of Geology and Palaeontology, Technical University of Clausthal (Clausthal-Zellerfeld, Germany); positive imprints of the specimens IGP In 190 (bearing the collector number F 15) and IGP In 191 (bearing the collector number F 51) are temporarily housed in Michael Sowiak's private collection (Glandorf, Germany)**;** both specimens were discovered by the amateur palaeontologist Michael Sowiak.

Description.—Specimen IGP In 190 (holotype; Figs 1,2): positive and negative imprint of an incomplete right wing; base, posterior wing margin, and apical area missing; as preserved, length about 64 mm, width about 24 mm; estimated length ranging between 85 and 100 mm; anterior wing margin strong; area between anterior wing margin and ScP broad (3.8 mm opposite the divergence of MA and MP + CuA); ScP gives off oblique anterior branches; R and RA not clearly visible, folded below ScP; RP diverges from R about 22 mm from wing base; as preserved, RP simple; RP briefly connected to anterior branch of MA about 5.4 mm distal to its point of divergence from R; M + CuA convex; MA branched 7.2 mm distal to its divergence from MP + CuA; anterior branch of MA diverging obliquely, briefly connected with RP, and diverges from it; as preserved, both branches of MA simple; MP and CuA (diverging from M + CuA) form a composite convex stem; MP diverges from it at the point of connection of MP + CuA with CuPa; free part of MP strongly concave; as preserved, MP and CuA + CuPa simple; CuA + CuPa convex; CuP branched about 14 mm distal to wing base; CuPa about 11.7 mm long before fusing with CuA; CuPb branched about 20.7 mm distal to its point of divergence from CuP; CuP, CuPa and CuPb concave; in the distal half of the preserved remains, RA, RP, branches of MA, MP, and CuA + CuPa, straight and almost parallel to the anterior wing margin; AA1 simple, convex; area between AA1 and the next AA vein broad; anal area broad; in areas between RA and RP, and CuPb and AA1, crossveins loosely arranged in intercalary convex secondary veins.

Specimen IGP In 191 (Fig. 3): positive and negative imprint of the apex of a wing; preserved length about 29 mm, preserved width about 21 mm; area between anterior wing margin and ScP very narrow; ScP reaching anterior wing margin; RA with a main fork and posterior veinlets vanishing in the area between RA and (anterior branch of?) RP; area between RA and (anterior branch of?) RP broad (4.2 mm opposite the fork of RA); RP(?) simple; MA with several branches; in areas between (branches of?) RP and branches of M, crossveins arranged in convex intercalary secondary veins.

Geological settings.— Both specimens were collected from the Westphalian D (Pennsylvanian) sequence in the Piesberg quarry, north of Osnabrück (Lower Saxony; Germany); the holotype specimen was provided by the upper layer of the seam "Flöz Zweibänke"

(Westphalian C/D boundary); the paratype was from the upper layer of the seam "Flöz Mittel" (Westphalian D) (Brauckmann & Herd 2003; see also Köwing & Rabitz 2005).

Discussion.— The specimen IGP In 191 is tentatively assigned to the same species as the specimen IGP In 190, due to its large size, and a similar cross-venation pattern. Some palaeopteran species contemporaneous to *kiarae sp. nov.* reached large sizes, but the occurrence of a branched RA and the absence of a clearly convex MA, suggest that the specimen IGP In 191 belongs to a neopteran species, such as *kiarae sp. nov.* In addition, both specimens were collected from the same locality. Therefore, the assignment of the specimen IGP In 191 to *kiarae sp. nov.* is plausible, but not ascertained. The very broad area between RA and RP (or its anterior branch) is troubling, as this area is not particularly broad in the specimen IGP In 190 (Fig. 1). If the specimen actually belongs to *kiarae sp. nov.*, it might be a forewing then (assuming that IGP In 190 is a hind wing; see below). The specimens IGP In 191 will not be considered further in this discussion.

We interpret the vein remnant, indicated by the sign '°' on Figs 1-2, as the anterior branch of MA, based on the strength of this structure. It is unlikely that it could be a crossvein, as other structures interpretable as crossveins are not visible at all in this area. Although the base of this presumed anterior branch of MA is not visible/preserved, the only plausible interpretation is that it is an actual main vein.

In the first instance, due to its incompleteness, it is not evident whether the holotype specimen is a fore or a hind wing. Because of the broad AA area (and the orientation of CuA + CuPa with respect to the anterior wing margin), we suggest that this is a hind wing.

The medio-cubital area is organized with a convex stem (M + CuA on Figs 1 and 2) from which diverges a posterior convex stem [as it is, CuA (+ MP, see below)] that fuses with the anterior branch of a concave vein (as it is, CuPa). When occurring in forewings, this character state characterizes an *Archaeorthoptera* (Béthoux 2007d). As far as reported, all Palaeozoic *Archaeorthoptera* that have a complete fusion of CuA with CuPa in their hind wings, also have it in forewings. Hence, according to the definition of *Archaeorthoptera* and our knowledge of the group, *kiarae sp. nov.* belongs to this taxon.

But the interpretation of the medio-cubital area in *kiarae sp. nov.* must be discussed with details. According to Béthoux & Nel (2002), in *Archaeorthoptera*, the convex CuA diverges from M and fuses with CuPa, resulting in a convex composite stem CuA + CuPa. However, in the hind wing of *kiarae sp. nov.*, a concave stem diverges anteriorly at the point of connection of CuA and CuPa (this stem is indicated as MP on Fig. 2). This implies that a concave vein sector is fused with CuA when it diverges from M. The only concave sector anterior to CuA is MP. Therefore M + CuA splits into MA and MP + CuA, (indicated by * on Figs 1,2) and MP diverges from MP + CuA at the point where CuA fuses with CuPa. According to the hind wing morphology of *dumasii* (see Béthoux 2003), this is a derived condition.

This area is known in a few lobeattid insects. In hind wings of *elongata* Brongniart, 1893: 433, (see Béthoux & Nel 2004: fig. 9) CuA is apparently very short. It cannot be ruled out that the visible part of M actually diverges at the point of connection of M + CuA and CuPa. However, the condition in *kiarae sp. nov.* is different, in that a part of M runs fused with CuA and later diverges. In hind wings of the lobeattid species *bronsoni* Dana, 1864 (see Béthoux 2008a: fig. 3) as well as in the cnemidolestodean species *gaudryi* Brongniart, 1885 (see Béthoux & Nel 2004: fig. 15) there is no evidence of a stem of M diverging at CuA + CuPa.

A common stem MP + CuA is known in caloneurodeans (fore and hind wings; see Béthoux *et al.* 2004) and *Gigatitanidae nom.* Sharov, 1968 *dis.-typ.* Béthoux, 2007d (forewings only; see Sharov 1968). However relationships with these groups can be excluded because *kiarae sp. nov.* lacks the branching of CuPa diagnostic of the panorthopterans, to which belong caloneurodeans and *Gigatitanidae*. In addition, caloneurodeans lack a developed vannus (see Béthoux *et al.* 2004; as opposed to the condition exhibited by *kiarae sp. nov.*), and the taxon *Gigatitanidae* is recorded only in the Triassic (with well-identified relatives in the Permian; Béthoux 2007d), with MP being actually distinct from CuA in hind wings. In summary, the occurrence of a common stem MP + CuA in hind wings of *kiarae sp. nov.* is challenging.

Another unusual feature is the brief connection of the anterior branch of MA with RP. There is no such connection in the lobeattid species *elongata* (see Béthoux & Nel 2004: fig. 9) and *cubitalis* (see Béthoux 2005b: fig. 5). In the cnemidolestodean species *gaudryi* (see Béthoux & Nel 2004: fig. 15) all branches of M are distinct from RP. A common stem RP + M is known in hind wings of gerarids (see Béthoux & Nel 2003), and a common stem RP + MA occurs in some genuine orthopterans such as elcanids (see Sharov 1968: fig. 13). But gerarids and elcanids exhibit a branched CuPa, qualifying them as more derived with respect to *kiarae. sp. nov.* In addition gerarids exhibit a connection of the whole stem of M with RP, and elcanids a connection of the whole MA with RP. These conditions arguably differ from a connection of the anterior branch of MA with RP, as exhibited by *kiarae sp. nov.* Even if one assumes that the remnant indicated by '°' on Figs 1,2 is not of main-vein origin, a RP forked near its origin with two branches simple for a long distance, would equally be an unique condition among Palaeozoic *Archaeorthoptera*, in the hind wing of which RP is usually branched just basal or distal to its midlength, and is provided with numerous branches.

In hind wings of the lobeattid species *bronsoni*, *elongata*, and *cubitalis* (see references above), CuA + CuPa is branched basal to, or near its midlength. This is also the case of the cnemidolestodean species *gaudryi*. Although the material of *kiarae sp. nov.* is incomplete, it can be determined that CuA + CuPa is simple for a long distance, most probably exceeding its midlength.

The cross-venation organization in *kiarae sp. nov.*, with weakly constrained secondary intercalary veins, has not been recorded in known Pennsylvanian *Archaeorthoptera* [there is no evidence of membrane alteration (disruption or overlap resulting from folding) in the area posterior to CuA, therefore no taphonomic bias could have affected observation of this feature in this area]. The condition of CuPb in hind wings (branched or simple) is unknown in most Palaeozoic *Archaeorthoptera*. This vein is simple in hind wings of genuine orthopterans (Sharov 1968), but branched in gerarids (Béthoux & Nel 2003) as well as in *kiarae sp. nov.*

The size of the species is also remarkable, with an estimated total hind-wing length ranging between 85 and 100 mm. Hind wings of *dumasii* do not exceed 75 mm (Béthoux 2003); *spilopterus* forewings do not exceed 80 mm, lobeattid forewings do not exceed 70 mm, and cnemidolestodean forewings do not exceed 60 mm (Béthoux 2005b, 2006; Béthoux & Nel 2004; in all cases hind wings are shorter than forewings). According to its estimated hind-wing length the species *kiarae sp. nov.* is actually the biggest known Pennsylvanian *Archaeorthoptera*, and one of the biggest insects ever.

In summary, the combination of a simple CuPa, a common stem MP + CuA (diverging from M + CuA), a brief connection of the anterior branch of MA with RP, and of a branched CuPb, picture a hind wing that challenges assignment to any of the known Palaeozoic *Archaeorthoptera*. Even if one assumes that the holotype is actually a forewing, this combination of character state would be unique: the MP + CuA common stem is shared with caloneurodeans, but the simple CuPa, the branched CuPb, and the cross-venation organization ('crossveins organized in secondary intercalary veins', as opposed to 'crossveins rarely reticulated' in caloneurodeans) do not comply with such an assignment. Relationships with Triassic *Gigatitanidae*, exhibiting such a feature, can be excluded, notably because *kiarae sp. nov.* exhibits a simple CuPa (this vein is abundantly branched in *Gigatitanidae*; see Béthoux 2007d). In addition *kiarae sp. nov.* would lack the stridulatory apparatus present in forewings of *Titanopterida* Béthoux 2007d, to which belong the *Gigatitanidae*. Finally, cnemidolestodeans exhibit a posterior branch of M (MP?) vanishing or fusing distally with CuA + CuPa in forewings (see Béthoux & Nel 2004). It is not excluded that the more derived representatives of the group could have a common stem MP + CuA, but assuming so, MP never diverges from MP + CuA, as opposed to the condition exhibited by *kiarae sp. nov.* Therefore, based on the unique combination of features of the holotype, the erection of a new species is justified.

The general habitus of *kiarae sp. nov.* hind wings is similar to that of some phasmatodeans (large size, and narrow remigium filled with veins simple and almost parallel to the wing margin for a long distance; see Ragge 1955). Affinity of *kiarae sp. nov.* with phasmatodeans, up to now reported from the Triassic (Nel *et al.* 2004, Sharov 1968) or Permian [(according to Gorokhov (1994); Gorokhov & Rasnitsyn (2002); but see Tilgner (2000)], must be considered as a working hypothesis. But until the wing venation of phasmatodeans is re-investigated (OB, in prep.), a more conclusive statement on the phylogenetic position of *kiarae sp. nov.* is out of reach.

Conclusion

Within the last twenty years 21 new insect species were described from the Piesberg locality (Brauckmann & Herd 2003, 2006; Zessin 2006). These discoveries supplement our comparatively poor knowledge of Pennsylvanian insect faunas. The discovery of *kiarae sp. nov.* demonstrates that a number of unknown and challenging lineages awaits to be unearthed. Excavations at the active Piesberg quarry and description of new findings are ongoing activities, with the hope of discovering additional data on *kiarae sp. nov.*

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Appendix

Forfexala gen. nov.

Type species.— *Forfexala kiarae sp. nov.*

Etymology.— After "forfex ", scissors in Latin, according to the morphology of the medio-cubital area in the (presumed) hind wing of the species and after "ala", wing in Latin (feminine gender).

Composition.— *Forfexala kiarae sp. nov.*

Diagnosis.— By monotypy, that of the type species.

Discussion.— Because the species *Forfexala kiarae* sp. nov. cannot be assigned to any of the known Archaeorthoptera genera (*i.e.*, the diagnosis of the type species distinguishes it from any other known genus), a new genus is erected.

Forfexala kiarae sp. nov.

Figs 1-3

Etymology.— After 'Kiara', name of the granddaughter of the discoverer of the material (Michael Sowiak) (genitive feminine).

Diagnosis.— Hind wing: length of at least 85 mm; RP simple for a long distance; anterior branch of MA briefly connected to RP; M + CuA separated into MA and MP + CuA; MP diverges from MP + CuA at the point of connection with CuPa; CuPb branched; cross-venation network loose, with intercalary secondary veins.

Material.— Specimen IGP In 190 (holotype), negative imprint, and specimen IGP In 191 (wing fragment; tentatively assigned to *kiarae sp. nov.*, see below), negative imprint, both housed at the Institute of Geology and Palaeontology, Technical University of Clausthal (Clausthal-Zellerfeld, Germany).

Description.— See above.